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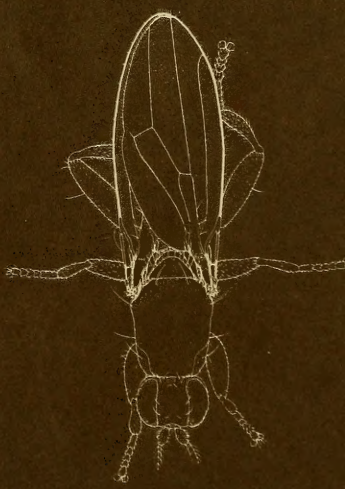

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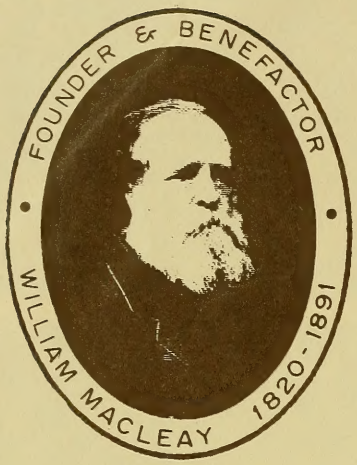

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Quartz Veining in Multiply-folded Greywackes, Bermagui, New South Wales, Australia

PAUL G. LENNOX
(Communicated by JEAN J. CARTER)

LENNOX, P. G. Quartz veining in multiply-folded greywackes, Bermagui, New South Wales, Australia. *Proc. Linn. Soc. N.S.W.* 112 (1), 1990: 1-14.

Quartz veins subparallel and subnormal to fold axes dominate veining at Bermagui. The widespread development of stripy cleavage (S_1) has enabled the timing between this cleavage and quartz veining to be better constrained than any other relationship. Most quartz veins have formed syn-S_1, but some developed throughout the deformation history.

Oxygen isotope studies and preliminary fluid inclusion studies indicate temperatures around 300°C, consistent with the greenschist facies mineralogy. The high and uniform $\delta^{18}0$ values indicate deposition of quartz over a narrow temperature interval from a fluid reservoir in the greywacke pile. These quartz-bearing fluids were mobilized during widely-separated orogenies in the Siluro-Devonian and early Carboniferous

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INTRODUCTION

Different interpretations have been made of the deformation history of the undifferentiated Ordovician greywackes and slate at Bermagui. Williams (1972) proposed a two phase deformation history and Powell (1983) proposed a five-phase model. Discussion of quartz veining within the context of these models was limited. Williams (1972) recognized the importance of quartz migration to the development of different foliation morphologies, but did not consider quartz veining within this model. Powell and Rickard (1985) identified some quartz veins as post-S_0, pre-S* and pre-S_1, as the quartz veins were isoclinally microfolded, with S* axial planar, and these veins were dissolved along S_1 surfaces. Studies of deformed coastal Ordovician sequences in northeast Victoria indicated that quartz veins formed pre- and post-S* (Wilson and Hedouville, 1985, figs 3d, 8).

This study clarifies the relationship between quartz veining and the folds and foliations in two coastal exposures at Bermagui. One of these exposures contains F_1 folds, while the other exposure exhibits F_1 to F_4 folds, enabling partial understanding of the geometrical and temporal relationship between quartz veining and folding-foliation development. The irregular development of quartz veins, and the rarity of suitable cross-cutting quartz veins, prevents complete resolution of the temporal relationships.

Regional and Local Geology

The mesoscopic folds containing quartz veins crop out at Bermagui in Ordovician greywacke and slate on the eastern margin of the Lachlan Fold Belt. This greywacke sequence has been subjected to greenschist facies metamorphism (Williams, 1971).

Williams (1971) recognized two generations of folds, with the meridional regional folds having an antiformal crest just offshore from Bermagui headland (Fig. 1) and a synformal crest about one and a half kilometres inland. This regional fold pattern was interpreted to be a second-generation structure. These later folds either refolded earlier folds to a recumbent attitude or reduced the interlimb angle of the earlier folds. Recumbent F_1 folds generally occur on the limbs of F_2 folds and isoclinal F_1 folds generally

occur in the hinge of F_2 folds (Williams, 1971). Powell (1983) recognized five phases of deformation at Bermagui. The first phase resulted in the development of a foliation without exposed folds (Powell and Rickard, 1985) whilst the second to fourth phases resulted in folds with foliations and the last phase resulted in kinking.

This study concentrated on two localities, the headland just east of the breakwater at Bermagui and the wave-cut platform and cliff on the north side of Zane Grey Pool about two kilometres south of Bermagui (Fig. 1; Powell, 1983). Remapping of foreshore exposures confirms the overall geology as reported by Powell (1983, figs 52, 53). The greywackes on the headland adjacent to the breakwater exhibit one generation of asymmetric, east-verging, upright mesoscopic folds (half wavelength ~ 5-7m) with axial surface differentiated crenulation cleavage (stripy cleavage, Figs 4**a**, **b**). The sandstone beds hosting quartz veins are usually less than half a metre thick and rarely up to one metre thick. The sequence north of Zane Grey Pool exhibits three generations of mesoscopic folds (F_1, F_2, F_3) varying from upright to recumbent (half wavelength ~ 5-7 m), with axial surface differentiated crenulation cleavage (stripy cleavage, S_1) or mm- to cm-spaced crenulation cleavage (S_2, S_3).

The F_1 folds at Zane Grey Pool have been refolded co-axially to form gently-plunging, upright to overturned asymmetric folds with overprinting axial surface spaced crenulation cleavage (Fig. 3**a**). The wave-cut platform exhibits both fold- and fault-related quartz veining. There are far fewer quartz veins and less variety of orientations of quartz veins at Zane Grey Pool exposures compared with the Bermagui headland exposures.

Poles to bedding for the Bermagui headland indicate that the upright F_1 folds plunge gently to the north-northeast (Fig. 2**a**). The contoured stereographic projection of poles to bedding for Zane Grey Pool indicates that F_2 plunge gently southsouthwest, and are thus coaxial with F_1 folds (Fig. 2**b**). The plots of foliations demonstrate that the stripy cleavage identified on Bermagui headland (Fig. 2**c**), which is axial planar to F_1 folds, has been folded about F_2 folds, and the S_2 and S_3 spaced crenulation cleavages are oriented either northwest-southeast or northeast-southwest (Fig. 2**d**). These stereographic projections support the field observations that F_1 folds were coaxially refolded by F_2 folds and neither of these two earlier fold phases is significantly affected by F_3 or F_4 folds or later kinking.

Methods and Methodology

Quartz Veining

In folded greywackes at both localities it is possible to define quartz-vein sets consisting of clusters of quartz veins of a similar size and orientation within the 0.5-1.0m thick, arenite beds. In up to 5m-wide sections across the hinge zone or limbs of these folds, representative quartz veins from a set were measured, and their cross-cutting relationships to other sets were established wherever possible.

Any sets striking 22.5° either side of the hinge line trend are considered subparallel sets (P sets), any sets 22.5° either side of normal to the hinge line trend are considered subnormal sets (N sets) and any sets intermediate between these are considered oblique sets (0 sets). Temporal relationships were established on the basis of four main types of intersections: 1) one set truncates another, 2) one set cuts the other with visible displacement, 3) one set cuts another without visible displacement, but fibres in one set are continuous across that vein at the intersection or 4) one set cuts another without visible displacement, fibres or any other diagnostic criterion. The overall sequence of sets from a number of exposures of the same limb or hinge zone was determined using a three by three matrix. This relates the number of sets doing the cutting on the abscissa to the

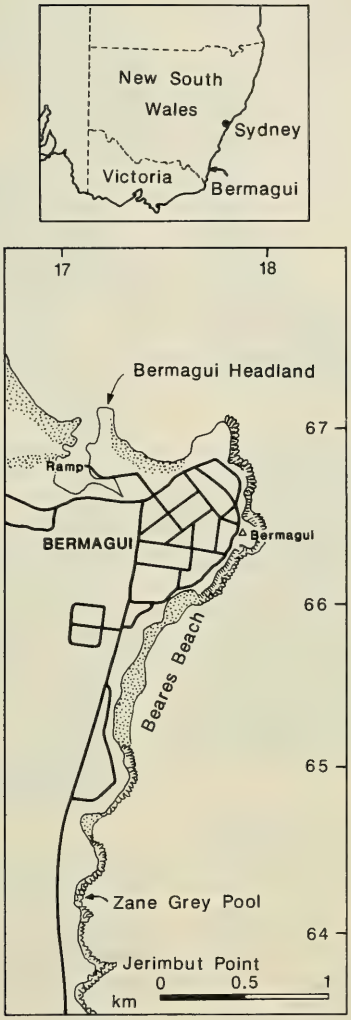

Fig. 1. Locality map showing the position of Bermagui on the New South Wales south coast and the named headlands at Bermagui.

number of sets being cut on the ordinate. This method provides an unambiguous guide to the order of formation of different sets.

There are planar and *en echelon* N, P and O quartz veins at Bermagui. There is also contemporaneous development of quartz veins at an angle less than 45° to the planar O, P and N sets. These are called conjugate sets to indicate their relationship to the nominated set.

The Zane Grey Pool quartz veins are dominantly planar N and P sets (Fig. 3) and rarely *en echelon* N and P sets. On Bermagui headland there are planar O, N and P sets occasional *en echelon* N and O sets (Figs 4 and 5) and rare quartz veins conjugate to the planar O, N and P sets (Figs 5**a**, **d**, Table 1).

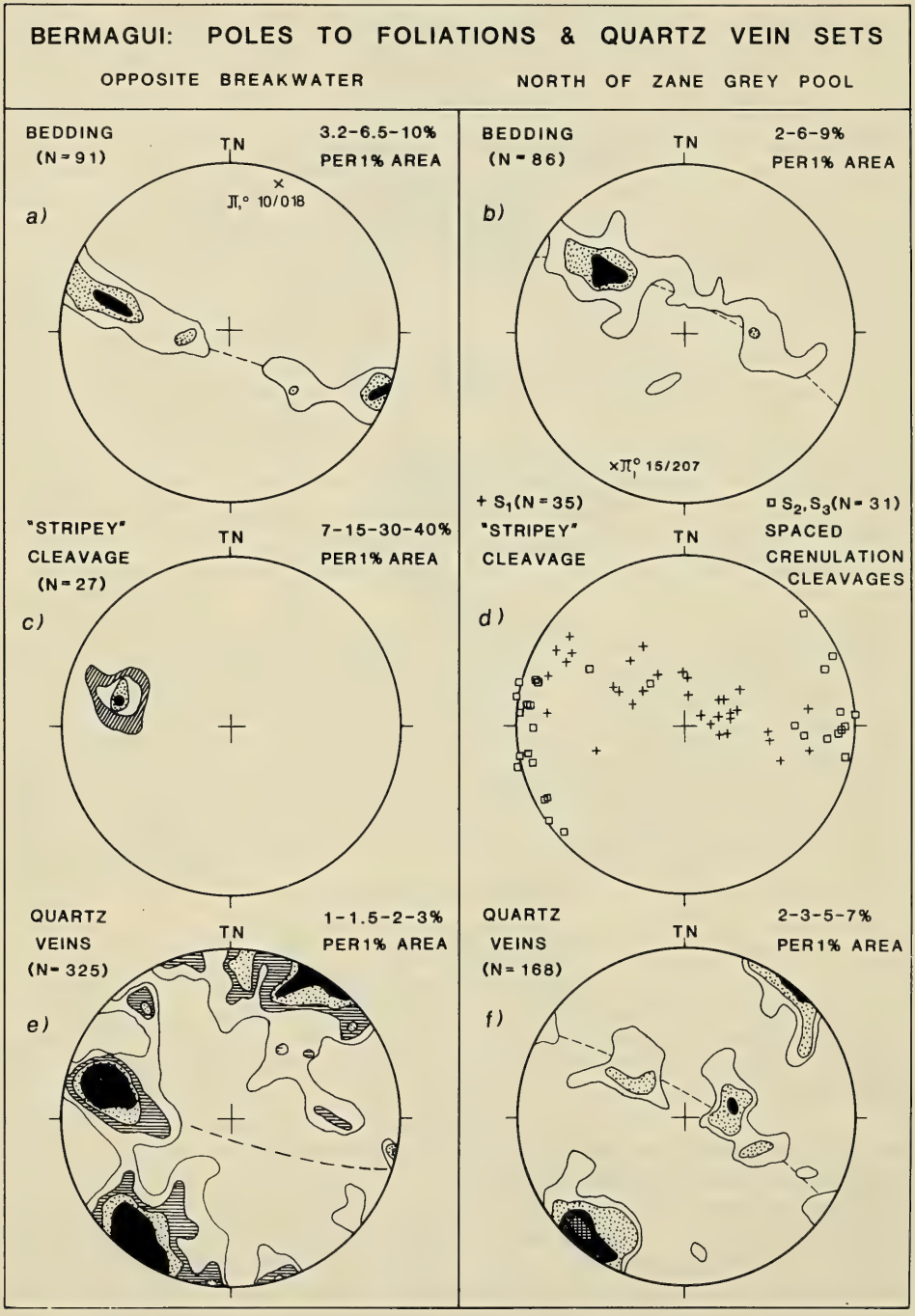

Fig. 2. Contoured stereographic projection (lower hemisphere) of poles to bedding (a, b), cleavages (c, d) and quartz veins (e, f) for Bermagui headland opposite the breakwater and north of Zane Grey Pool. N = number of readings.

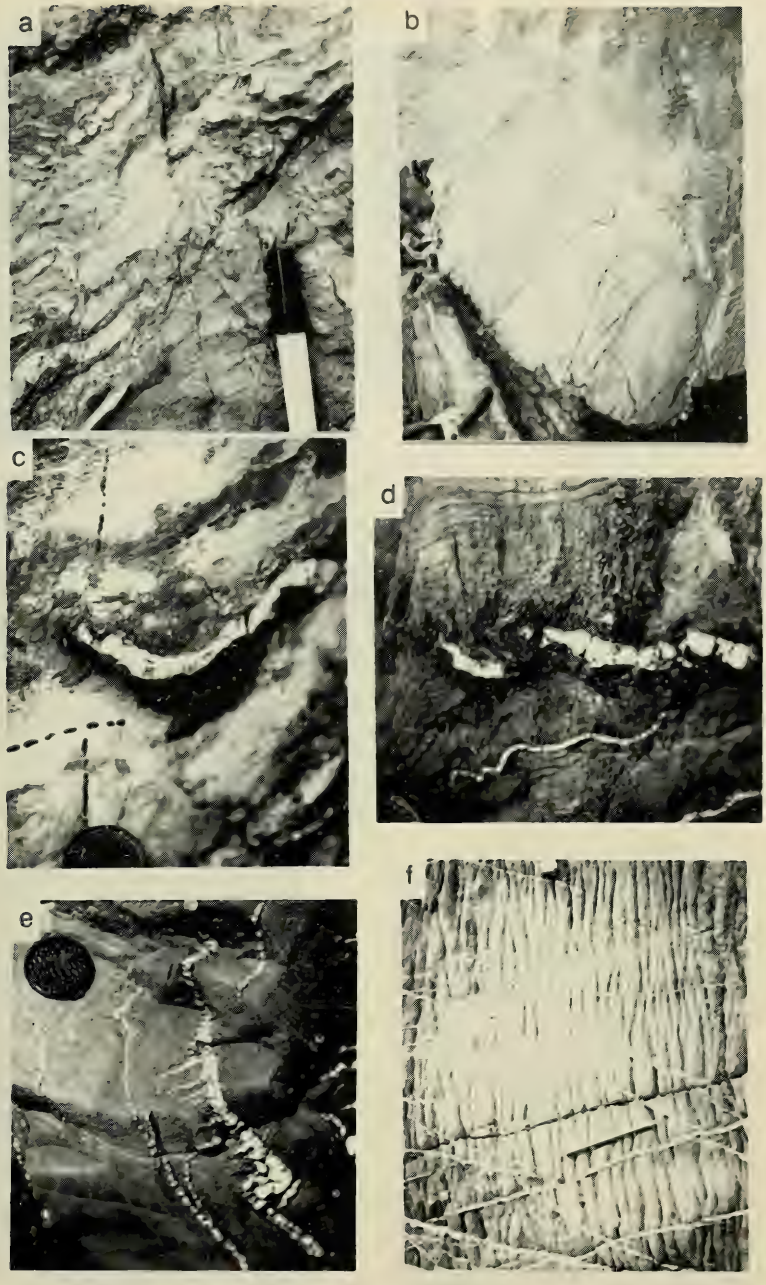

Fig. 3. Quartz veins and foliations at Zane Grey Pool. **(a)** Bedding trends top right to lower left and spaced crenulation cleavage trends top to bottom. The S* cleavage trends left to right and intersects the bedding at a low angle and is partly defined by quartz veins. Black marking pen cap is 45mm long. **(b)** Limb to hinge zone of inclined F_1 fold with fanned stripy cleavage and extensional P quartz veins. Lens cap is 50mm across. **(c)** Folded quartz vein with spaced crenulation cleavage axial surface to open fold (solid line). The dashed line is parallel to bedding. Lens cap is 50mm across. **(d)** *En echelon* P quartz veins disrupt S*, S_3 and S_4 foliations. The quartz vein at left of centre is 50mm long. **(e)** P quartz veins with pinnate branches on the limb of an F_1 fold. Lens cap is 50mm across. **(f)** Prominent stripy cleavage from top to bottom is dissected by conjugate N quartz veins. Scale has 10mm divisions.

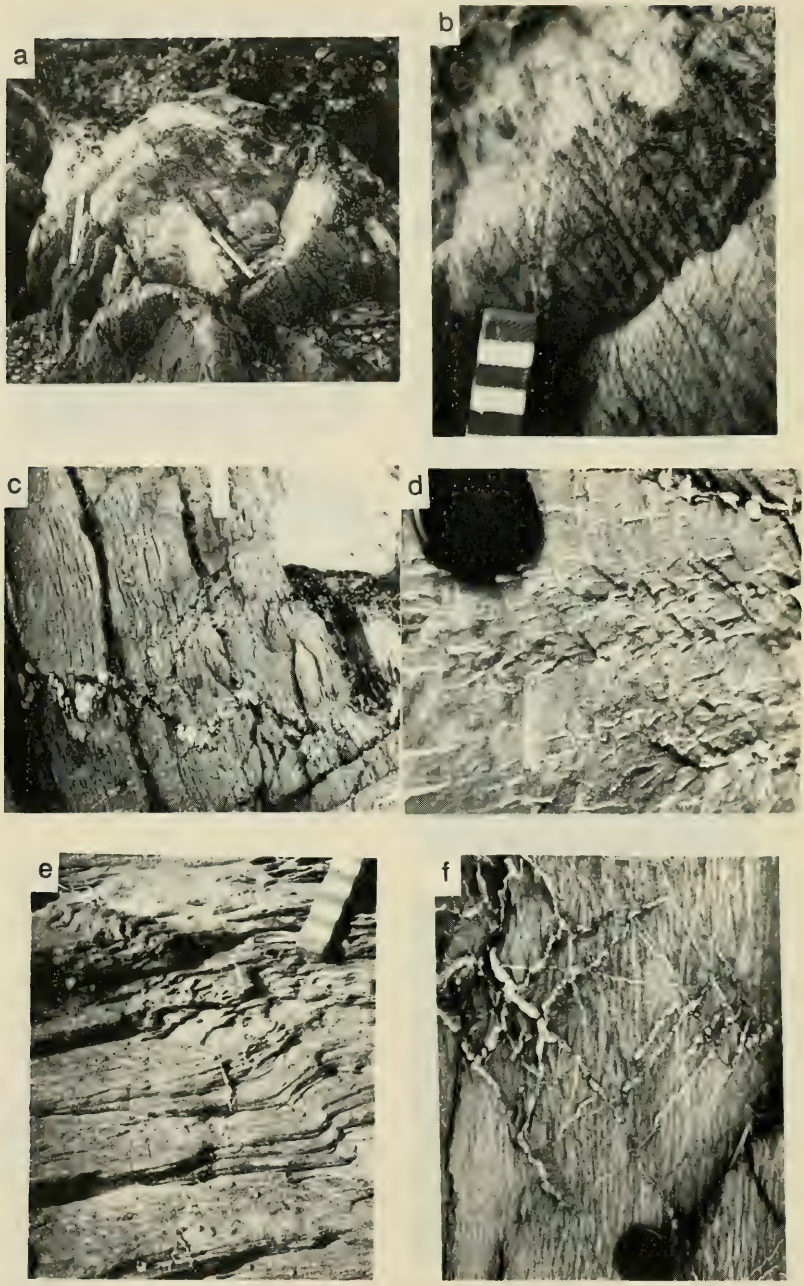

Fig. 4. Folds, kinks, quartz veins and stripy cleavage at Bermagui headland. **(a)** Asymmetric F_1 fold with axial surface stripy cleavage (see **b**). Scale has 10mm divisions. **(b)** Close up view of stripy cleavage (upper left to lower right) and bedding (lower left to upper right) on the limb of an F_1 fold. Scale has 10mm divisions. **(c)** Stripy cleavage (top to bottom) dissected by folded N quartz vein. Scale has 10mm divisions. **(d)** Stripy cleavage dissecting *en echelon* N veins. Lens cap is 50mm across. **(e)** *En echelon* N veins pass through kink without deflection. Scale divisions are 10mm. **(f)** Stripy cleavage from top to bottom. There are two O sets one trending top right to lower left (O_1) and the other trending top left to lower right (O_2). The O_1 set shows microfolding and dissection by the stripy cleavage. Lens cap is 50mm across.

Oxygen Isotope Studies

A study of the oxygen isotope relationship between variously oriented quartz veins in the limbs and hinge zone of F_1 folds at Bermagui headland and in F_1 and F_2 folds at Zane Grey Pool was carried out to determine the temperature and source of the fluid from which the quartz veins originated.

Oxygen isotope analyses of vein quartzes were performed at the University of Queensland using standard techniques (Clayton and Mayeda, 1963) and are reported in per mil relative to SMOW (Table 2). Using the quartz-water fractionation of Matsuhisa *et al.* (1979), fluid isotopic compositions were calculated from the mean values for quartz isotopic data at the model temperature 250-300°C (Tables 2 and 3). The errors in the fluid isotopic compositions reflect: (1) the range of quartz $\delta^{18}0$ values, at one standard deviation, and (2) the model temperature interval. This methodology should give maximum error values for the calculated fluid isotopic compositions because the range of mineral isotopic values reflects the temperature regime as well as the fluid composition during quartz veining.

Fluid Inclusion Studies

Over twenty quartz veins were sampled at Bermagui but only three proved to have fluid inclusions large enough for use on the heating stage. These inclusions appear to be primary and not secondary or pseudosecondary (Eadington and Wilkins, 1980). The two quartz veins from Bermagui headland were *en echelon* N and P veins shown by field examination to be syn- or post-F_1 and pre-F_2 (Fig. 6, C1 and $Q\phi$). The single vein from Zane Grey Pool is an *en echelon* N vein in a F_1 syncline and formed syn- or post-F_1 and pre-F_2 (Fig. 6, LLϕ). These veins are the dominant quartz veins at Bermagui.

Results

Quartz Veining

It is possible to construct a chronological sequence of development of cleavages and quartz veins for the Bermagui headland, and to a lesser extent for the Zane Grey Pool exposures. The widespread development of stripy cleavage (S_1) enables rapid assessment of the timing between quartz vein formation and stripy cleavage development. The dominant N and P sets on Bermagui headland show examples of dissolution of these quartz veins adjacent to the stripy cleavage (Figs 4**d**, **f**) and other instances where dissection has not occurred. Any quartz vein affected by the stripy cleavage must have formed pre- or early syn-S_1, whilst those quartz veins unaffected by the stripy cleavage must have formed post-S_1. In the few areas where kinking developed on Bermagui headland, P and N sets show rotation into the kink planes. There are rare instances where *en echelon* N quartz veins cross-cut a kink band and are affected by the kinking (Fig. 4**e**). Thus P and N quartz veins on Bermagui headland were mostly formed pre- to syn-S_1 and pre-kinking. Kinking occurred as the final event in the deformation history (Powell, 1983). Therefore it is not surprising that most of the quartz veins are formed pre-kinking. The mesoscopic folds on Bermagui headland are F_1 folds with axial planar stripy cleavage (Fig. 4**a**). If most quartz veins are pre- or syn-S_1 then this indicates that most quartz veins were formed pre- or syn-F_1.

From the limited number of quartz veins intersecting in the sequence at Zane Grey Pool, it can be shown that P sets usually cut N sets, although there are instances where N and P veins were formed contemporaneously (Fig. 5**b**) or where N veins cut P veins (Fig. 5**c**). Generally O sets cut P sets, leading to a simple three-stage sequence of sets formation, i.e. N to P to O. Since previous studies of more prolifically-developed quartz veins indicate extensive overlapping in the time of formation of O, P and N veins in

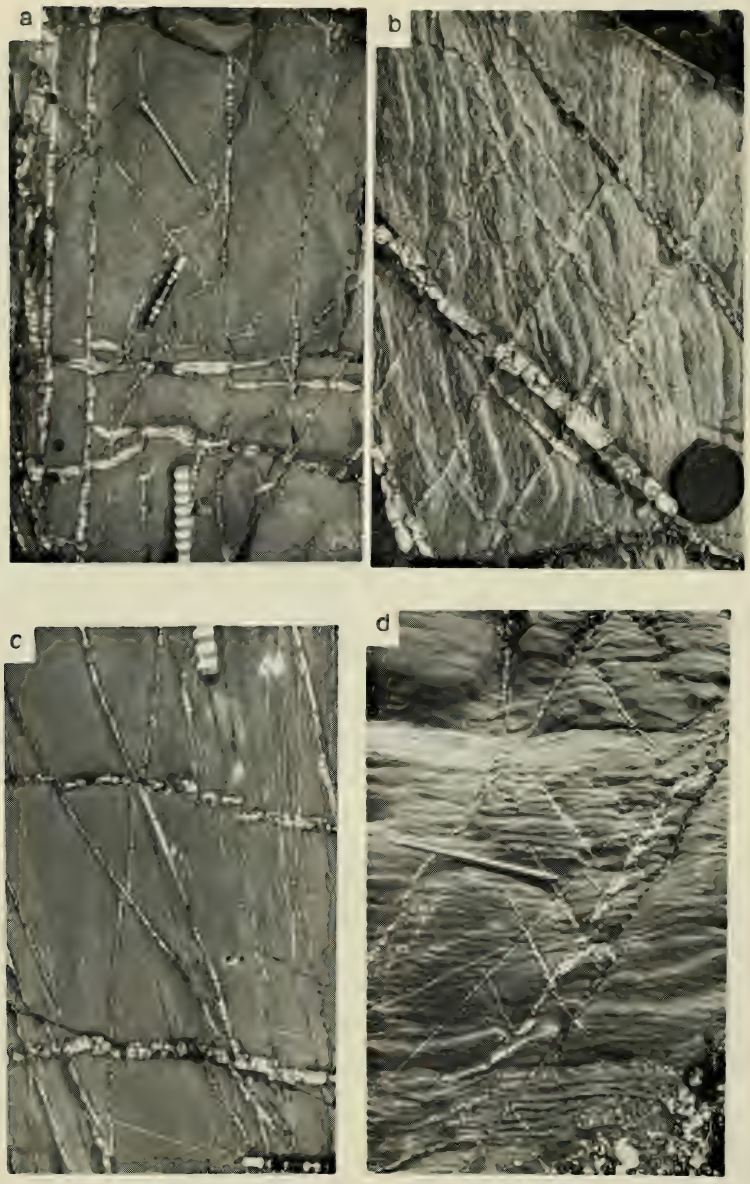

Fig. 5. Morphology and temporal relationships between quartz veins at Bermagui headland. **(a)** P veins (scale) formed syn- to post- the conjugate (pencil and texta) O veins. Note in the centre of the plate displacement of conjugate O veins (pencil). Scale has 10mm divisions. **(b)** Stripy cleavage — bedding intersection lineation trends top to bottom and is dissected by thicker N veins (middle left to bottom right) and thinner P veins (top right to lower left). Some N veins are cut by P veins and cut other P veins. Lens cap is 50mm across. **(c)** Scale parallel to F_1 fold axis and bisects the acute angle between conjugate O veins and is parallel to thin P veins. Thicker N veins show dissection in some areas (upper centre) and are not disrupted in other areas (bottom). Scale divisions are 10mm. **(d)** Stripy cleavage-bedding intersection lineation trends left to right. *En echelon* O sets trend top left to bottom right and conjugate planar to *en echelon* O sets trend top right to bottom left. Pencil is 150mm long.

simply folded greywacke sequences (Lennox, 1985; Lennox and Golding, 1989), it is extremely unlikely that this observed order of formation of quartz veins would rigorously apply in different parts of this multiply-folded sequence. The restricted development of F_3 and F_4 folds at Zane Grey Pool prevents an assessment of the relationship between quartz veining and these fold- and foliation-forming events. In rare instances open microfolded quartz veins were observed disrupting the S_1 cleavage in pelites. The S_2-spaced crenulation cleavage is axial surface to these microfolds (Fig. 3**c**). This indicates that some O quartz veins developed post-S_1 and pre- or syn-S_2. Other O and P quartz veins disrupt the S_1 to S_3 fabrics indicating formation post-S_3 (Fig. 3**d**). Normally O and P sets at Zane Grey Pool exposures are folded by mesoscopic F_1 folds or are microfolded by parasitic folds on the limbs of the mesoscopic F_1 folds. The stripy cleavage (S_1) dissects some O and N sets and is truncated by other O and N sets (Fig. 3**f**). Two O and N sets in the Zane Grey Pool exposures are pre- to syn- the first phase of folding and associated cleavage whereas P sets are commonly formed pre-F_1 folding. Some planar vein sets developed as extensional veins in the outer hinge zone of mesoscopic F_1 folds during folding (Fig. 3**b**) and other P veins on the limbs of mesoscopic F_1 folds exhibit pinnate branches indicating some reorientation of the stress field during quartz vein formation.

TABLE 1

Quartz vein abundances, Bermagui

Occurrence	Bermagui headland	Zane Grey Pool
rarely developed	P conjugate P *en echelon*	N *en echelon* P *en echelon*
common	N conjugate O *en echeon* O conjugate N *en echelon*	O conjugate O
abundant	P, N	P, N.

The contoured stereographic projections of poles to quartz veins for Bermagui headland shows three point populations indicative of P and N quartz veins (Fig. 2**e**). Coaxial refolding of F_1 folds would result in little apparent reorientation of N veins on a stereographic projection, because of their attitude to the pole of rotation whereas P veins would be rotated on a stereographic projection. Depending upon the mechanism of folding coaxial refolding may simply move populations of poles of P quartz veins around small circles (Ramsay, 1967). The contoured stereographic projection of poles to quartz veins for Zane Grey Pool is consistent with rotation of mainly P and N veins. This results in a scatter of point populations on the great circle girdle defined from the poles to bedding data indicative of differently-rotated P veins, along with a point concentration due to rotated, but geometrically little modified, N veins near the F_2 fold axis (Fig. 2**f**).

Oxygen Isotopes

Assuming a reasonable deposition temperature of 250-300°C (based on preliminary fluid inclusion data which suggest corrected homogenization temperatures around 300°C, and mineralogy), the calculated fluid composition is 7.2 ± 1.3 (250°C) and 9.1 ± 1.3 (300°C) (n = 21) consistent with metamorphic or magmatic fluids (Taylor, 1979).

The oxygen isotope composition of the quartz averages 16.2 ± 0.2 (n=21) which lies within the range of mean $\delta^{18}0$ for Victorian gold quartzes (15.8 to 20.2, Wilson and Golding, 1988) considered to have been derived from non-igneous ore fluids. The Cape Liptrap greywacke sequence which was folded by one phase of deformation contains quartz veins with comparable average oxygen isotope composition: 18.4 ± 0.4 (Lennox and Golding, 1989).

TABLE 2

Oxygen isotope data for quartz veins from Bermagui

Locality	Quartz Vein Type	Timing	$\delta^{18}0$ quartz per mil
Bermagui Headland	N	N cuts P	15.8
Fault Zone			16.3
	P	P cuts N	16.0
	P	pre-F_1	16.3
en echelon	P		16.3
F_1 fold	N		16.0
F_1 fold, *en echelon*	N		16.6
en echelon	O		16.0
conjugate	O		15.8
F_1 fold limb	O		16.2
F_1 fold	P	O cuts P	16.0
F_1 fold limb, *en echelon*	N		15.9
F_1 fold hinge zone	N		16.1
	P	N cuts P	16.1
Zane Grey Pool			
	P	pre-F_2	16.2
	P		16.4
	P	pre-F_2	16.6
F_2 fold	O		16.1
F_1 fold	O		16.0
	P	pre-F_1	16.0
F_1 fold hinge zone	N		16.5

These high and uniform $\delta^{18}0$ values imply deposition of all quartz over a narrow temperature interval from a fluid reservoir with constant $\delta^{18}0$ composition. This constancy is compatible with a metamorphic fluid regime, although a magmatic component cannot be discounted. The homogeneous calculated fluid suggest that local fluid-rock interaction with the diverse host lithologies at Bermagui has not significantly modified fluid composition. Conversely, fluid to rock ratios during deformation may have been sufficiently high to effect equilibration between the different rock types and the infiltrating fluid.

Fluid Inclusions

The average freezing point depressions, corrected homogenization temperatures and calculated fluid salinities are given in Table 4. The homogenization temperatures were corrected using the curves of Potter (1977) assuming a pressure of 200 MPa at the time of entrapment. The range of values for uncorrected homogenization temperature and freezing point depression for fluid inclusions from the three quartz veins are shown in Figs 6**a**, **b**. The salinities mean that the fluids from which the quartz veins were derived were poorly saline. Clathrates do not appear to be present in the system nor has the system boiled thus making P-T estimates difficult to determine (Eadington and

TABLE 3

Mean oxygen isotope compositions of quartz vein types, with calculated fluid compositions at 250-300° C

Locality/Vein type	Number of readings	$\delta^{18}0$ quartz $\pm$ 1δ (per mil)	Calculated $\delta^{18}0$ fluid $\pm$ (1.1 $\pm$1 δ)* (per mil) 300°C	250°C
Bermagui Headland				
N	5	16.1 ±0.3	9 ±1.4	7.2 ±1.4
P	5	16.0 ±0.2	9 ±1.3	7.1 ±1.3
O	3	16.0 ±0.2	8.9 ±1.3	7.0 ±1.3
Fault Zone	1	16.3	9.2	7.3
Total	14	16.1 ±0.2	9 ±1.3	7.1 ±1.3
Zane Grey Pool				
N	1	16.5	9.4	7.5
P	4	16.3 ±0.3	9.2 ±1.4	7.3 ±1.4
O	2	16.1 ±0.1	9 ±1.2	7.0 ±1.2
Total	7	16.3 ±0.2	9.2 ±1.3	7.3 ±1.3
Grand Total	21	16.2 ±0.2	9.1 ±1.3	7.2 ±1.3

* Fluid $\delta^{18}0$ values were calculated using the quartz-water fractionation determined by Matsuhisa *et al.* (1979). The equation for temperatures between 250 and 500°C is $1000 \ln \alpha = 3.34(10^6 T^{-2})-3.31$.

Wilkins, 1980). The corrected temperatures and pressures are consistent with previous estimates of the greenschist facies metamorphism which affected this rock sequence (Williams, 1972). Thus greenschist facies prograde metamorphism, quartz vein development and folding are contemporaneous events at Bermagui. Basic dyke rocks were sampled in an attempt to identify minerals and use univariant reactions marking transitions between various greenschist facies as a guide to P-T conditions (Liou *et al.*, 1985). These basic rocks have undergone metamorphism and now contain actinolite, chlorite, albite, epidote, calcite and white mica (Offler, pers. comm.), consistent with greenschist facies metamorphism. More sampling of quartz veins and a larger number of heating stage measurements would be required to more confidently constrain estimates of pressure and temperature during prograde metamorphism.

TABLE 4

Heating stage measurements and calculated fluid salinities calculated according to Roedder (1962)

Quartz Vein	Number of readings	Freezing point depression Average °C $\pm$1δ	Corrected Homogenization Temp. Average °C $\pm$1δ	Wt.% NaCl
C1	14	-5.7 ±4.9	303.8 ±45.8	+8.8 ±7.9
LLϕ	6	-2.1 ±1.8	312.0 ±7.2	+3.5 ±3.0
Qϕ	15	-2.3 ±1.7	341.2 ±11.1	+3.8 ±2.8

DISCUSSION

The abundance of P and N quartz veins at Bermagui reflects the dominance of a regional stress field during folding with σ_1 normal and σ_3 parallel to the developing fold axis. At this time N sets formed. The presence of a localized stress field in the outer arcs

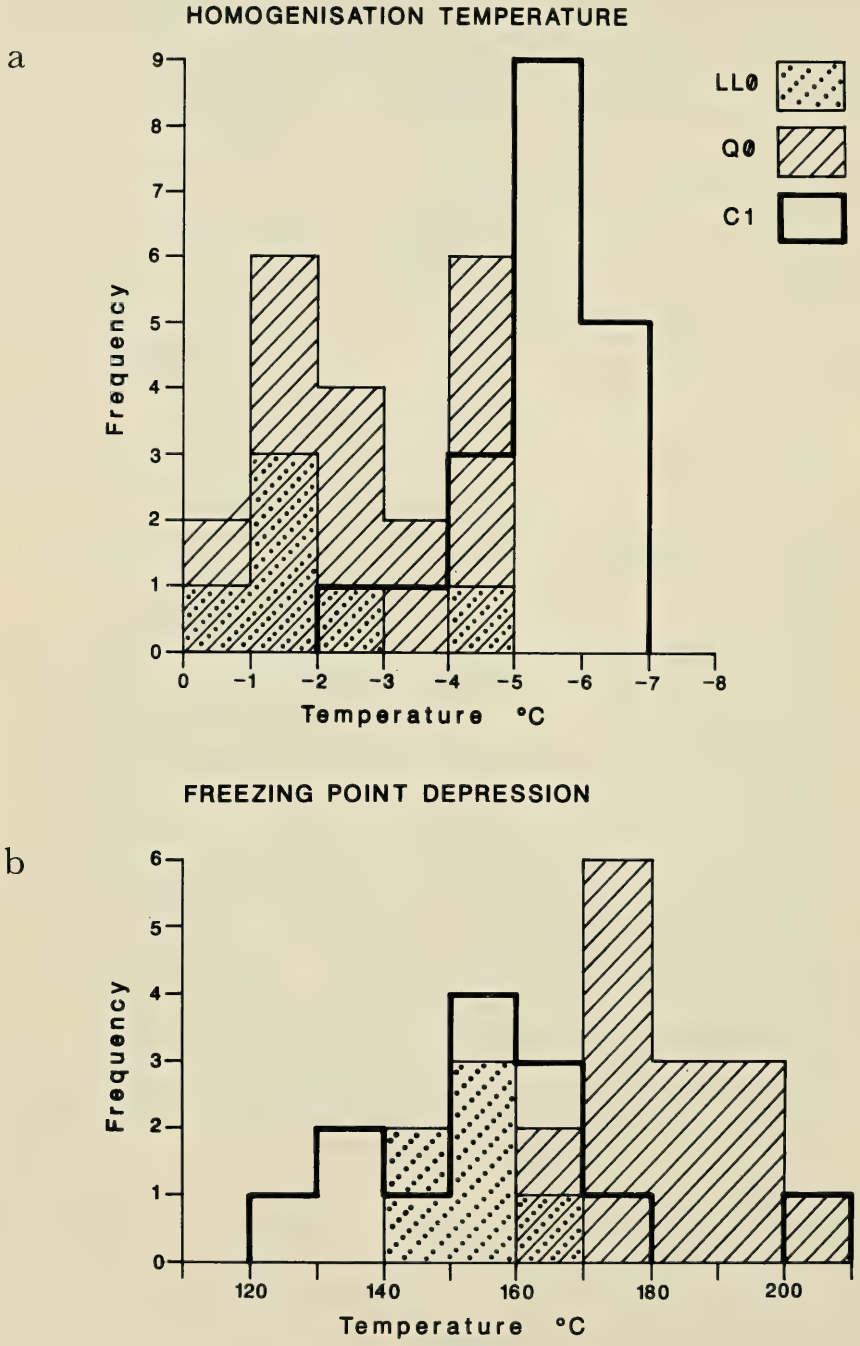

Fig. 6. Histograms **(a)** homogenization temperature for fluid inclusions from the three quartz veins. C1 and Qϕ are from Bermagui headland and LLϕ is from Zane Grey Pool. **(b)** The freezing point depression for the fluid inclusions from the same three quartz veins.

of the developing fold in which S_1 was parallel and S_3 normal to fold axis resulted in time P sets forming. This is comparable with the model proposed on the basis of a much more thorough study of quartz-veined folded greywackes at Cape Liptrap, Victoria (Lennox, 1986; Lennox and Golding, 1989).

The differences between the quartz vein formation in the refolded sequence at Bermagui headland and the multiply-folded sequence at Zane Grey Pool probably reflect the effects of the longer deformation history in the latter locality. The coaxial F_2 refolding at Zane Grey Pool permitted new N, P and O sets to form, whilst the areally restricted F_3 and F_4 folding phases provided more sites for quartz veins.

The presence at Bermagui of more quartz vein morphologies compared with the quartz veins at Cape Liptrap probably also reflects the more complicated multiple folding- and foliation-forming deformation history at Bermagui.

The high and uniform $\delta^{18}0$ values imply deposition of all quartzes over a narrow temperature interval from a fluid reservoir in the greywacke pile. Powell (1983) proposed that F_1 folds formed during the Bowning Orogeny (latest Silurian to earliest Devonian) whilst F_2 folds formed during the Kanimblan Orogeny (early Carboniferous). The oxygen isotope results indicate that fluids mobilized during these widely separated orogenies were similar.

The preliminary fluid inclusion results indicate that the pressure and temperature were around 200-300 MPa and around 300°C during quartz vein formation, consistent with the greenschist facies mineralogy of the greywacke sequence.

Acknowledgements

The Faculty of Applied Science, University of New South Wales financially assisted this project with two Special Projects Grants. Sue Golding, University of Queensland is thanked for organizing the oxygen isotope analyses. Peter Eadington and Robin Offler are thanked for guidance on fluid inclusions and low grade metamorphism respectively. Geoff Taylor kindly organized the heating stages to be in working order. Robin Offler and Steve Cox are thanked for constructive comments on the manuscript.

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Suburban Development and Resultant Changes in the Phosphorus Status of Soils in the Area of Ku-ring-gai, Sydney

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(Communicated by P. M. SELKIRK)

LEISHMAN, M. R. Suburban development and resultant changes in the phosphorus status of soils in the area of Ku-ring-gai, Sydney. *Proc. Linn. Soc. N.S.W.* 112 (1), 1990: 15-25.

Total phosphorus of urban bushland soils from the Ku-ring-gai area in the northern suburbs of Sydney was measured. Sampling sites were located on hillslopes, undeveloped ridgetops, adjacent to creeks and roads, downslope of suburban boundaries and stormwater outlets, and along sewerage lines. All sites were located on soils derived from Hawkesbury Sandstone. Within urban bush valleys, sites adjacent to nutrient sources had significantly higher phosphorus levels than sites remote from nutrient sources. Sites downslope of suburban boundaries were the least affected (average 90 ppm) while sites receiving urban runoff directly had the highest levels of phosphorus (e.g. downslope of stormwater outlets 438 ppm). The area of phosphorus enhancement around nutrient sources was largest for sites located downslope of any source. These results have important implications for the management of urban bushland and the control of exotic plant species.

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INTRODUCTION

Sydney is fortunate to have a substantial area of bushland reserves within the metropolitan area. These bushland areas are regarded as a valuable resource in an urban landscape (Buchanan, 1979; Schoer, 1983), offering important aesthetic, recreational and educational opportunities as well as providing habitat for flora and fauna. With continuing urban consolidation and expansion, these areas face increasing pressure due to their proximity to urban development.

Sydney soils are particularly noted for their low phosphorus level due to the low phosphate content of their parent material. Beadle (1962) reported total phosphate contents of Hawkesbury Sandstones of about 30-40 ppm. Several authors (Beadle 1953, 1954, 1962; Specht 1963, 1975) have suggested that soil fertility is the major determinant of the structure and composition of much of the Australian vegetation, with phosphorus implicated as the limiting nutrient. Some of these studies have also shown that the addition of phosphorus may greatly change the floristics of a community. A major problem in the management of urban bushland is the establishment of exotic, or weed species, which may be advantaged by these higher soil nutrient conditions. The low nutrient levels of the Hawkesbury Sandstone soils make these areas especially vulnerable to any addition of nutrients.

It is generally acknowledged that urban bushland receives an additional influx of nutrients from the surrounding suburban development. Dumped garden rubbish, septic tank effluent, sewage overflows, household drainage and stormwater runoff are thought to be the main contributors (Buchanan, 1979; Adamson, 1980; Clements, 1983). Several studies have also shown that stormwater runoff from urban areas contains significant amounts of sediment and soil nutrients (Bliss *et al.*, 1983; Wright, 1984).

Clements (1980, 1983) has reported higher phosphorus levels of soils from

suburban sites in the Sydney area compared to soils derived from similar parent lithology in non-suburban sites. She also found that high soil phosphorus levels were related to the presence of mesomorphic species, both native and exotic. Lambert and Turner (1987) found that overall phosphorus concentrations in leaves were higher in plants from sites near development than from undisturbed sites. The aim of this study was to investigate the distribution of soil phosphorus within urban bushland reserves, the relative contribution of specific nutrient sources to soil phosphorus levels and the extent and direction of the spread of soil phosphorus away from these sources. This knowledge will provide a sound basis for the design of management techniques to control exotic plant species in urban bushland.

Method

Site Description

All sites surveyed were within the area of the Municipality of Ku-ring-gai in the northern suburbs of Sydney (Fig. 1). The natural vegetation is typically open-forest, dominated by the *Angophora costata* association, and low woodland, dominated by the *Eucalyptus haemastoma* association (Buchanan 1983).

The area of Ku-ring-gai consists of a central ridge of Wianamatta Shale bounded on the east and west by Hawkesbury Sandstone (Little and Storrier, 1954, Fig. 1). All sites surveyed were on soils of the Hawkesbury Association. Surface soils of the Association are coarse-textured sands of variable depth; these are well-drained, acidic and of low fertility (Walker, 1960).

Sampling Strategy

The study was divided into four sections. The first was a preliminary survey of soil phosphorus distribution within a typical urban bushland valley. This was in order to identify whether phosphorus enrichment occurs generally throughout urban bushland, accumulates in distinct zones or is confined to concentrations around point sources. The results established that there was a significant difference in soil phosphorus levels between the locations sampled, with highest levels adjacent to nutrient sources. Consequently the remainder of the survey examined these nutrient sources to assess their relative contribution to soil phosphorus levels, and the extent and direction of the spread of soil phosphorus around these sources.

For each site the age of surrounding urban development was determined from aerial photographs and information provided by Ku-ring-gai Municipal Council. The location of sewerage lines and drainage easements was determined from Water Board maps and Ku-ring-gai cadastral maps respectively. The presence of each exotic plant species and the level of infestation (light, medium, heavy) was recorded at every site.

Section One

A valley 33 ha in area with an urban catchment of 112 ha (Buchanan, 1983) was chosen for the preliminary survey (valley 1 in Fig. 1). Five transects across the valley were selected by a block random method. Seven sites along each transect were sampled. These covered five site types: undeveloped ridgetop, hillslope below undeveloped ridgetop, suburban boundary, hillslope below suburban boundary, and the creek.

Section Two

Soil adjacent to three creeks in valley systems 1, 4 and 9 (Fig. 1) was sampled. The sites sampled satisfied the factor requirements of a three-way design with two replications. The factors were: individual creeks (three levels); distance from the creek bank

(five levels — 2m, 5m, 10m, 15m and 25m) and aspect (two levels — north and south facing). Slope of each transect was measured. Slope angles less than 15° were defined as moderate and greater than 15° as steep.

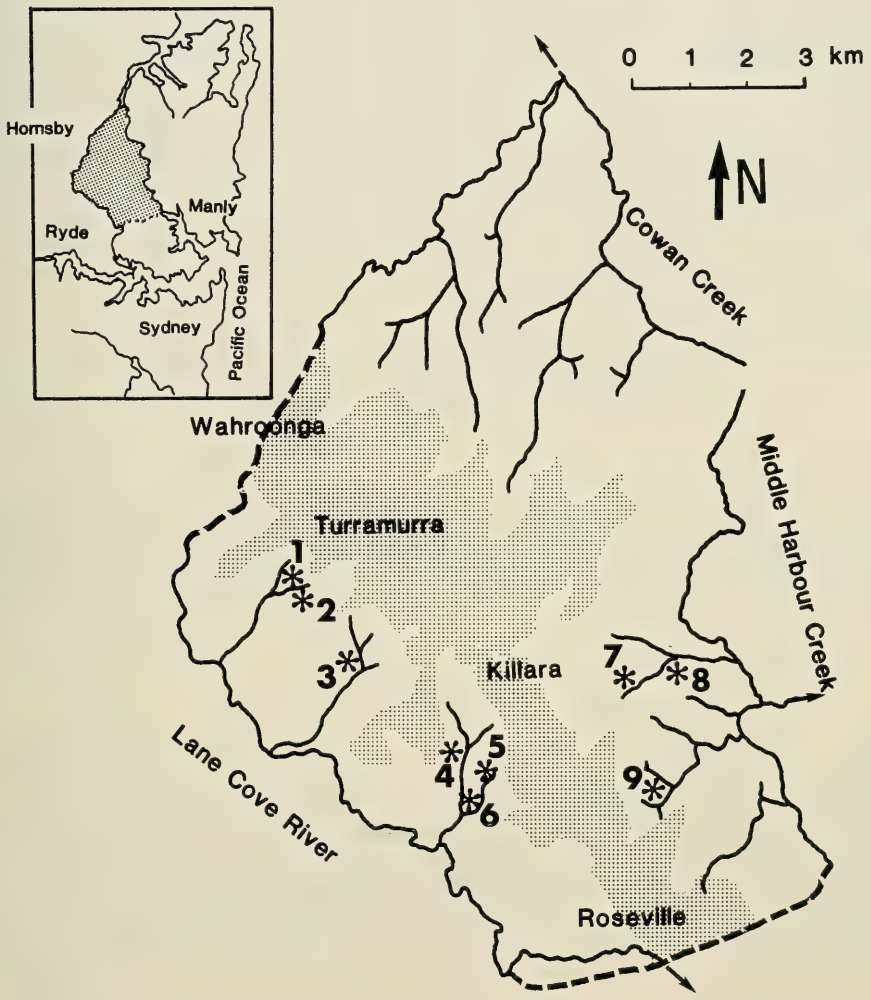

Fig. 1. Map of the area of Ku-ring-gai; the shaded area represents Wianamatta Shale and the unshaded area Hawkesbury Sandstone; * shows the location of valleys in which sampling sites were located. The arrows indicate the direction of flow of the streams. The numbers associated with each valley are referred to in the text.

Section Three

Soil adjacent to six suburban boundaries was sampled from valley systems 1,2,5 and 7 (Fig. 1). Sites sampled satisfied the requirements of a three-way design with two replications. The factors were: age of surrounding development (three levels — 35 years, 15 years and no development); distance from boundary (five levels — 5m, 10m, 20m, 30m and 40m) and aspect (two levels — north and south facing). The boundary was

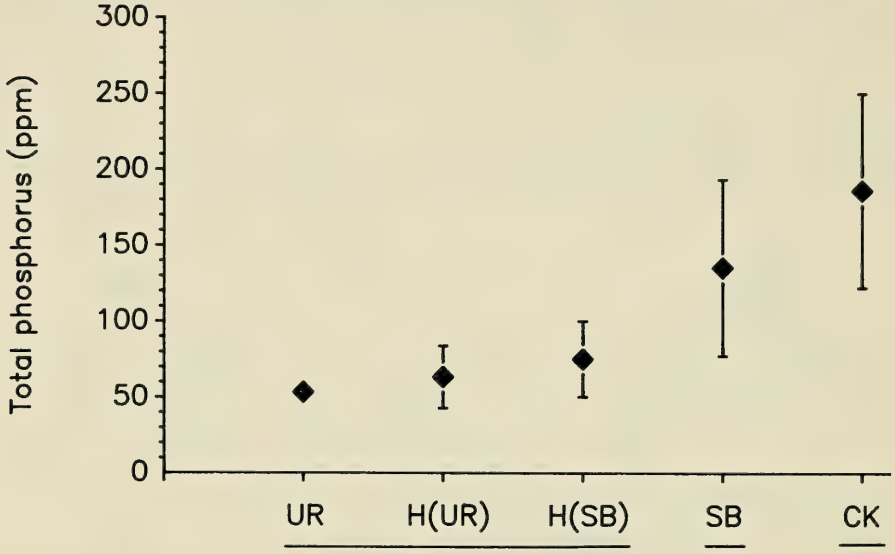

Fig. 2. The average total soil phosphorus of sites within an urban bush valley; UR undeveloped ridgetop; H(UR) hillslope below undeveloped ridgetop; H(SB) hillslope below suburban boundary; SB suburban boundary; CK creek. The error bar shows standard deviation. The solid lines below the x-axis indicate the groupings of phosphorus levels on site types determined by the SNK test ($\alpha = 0.05$).

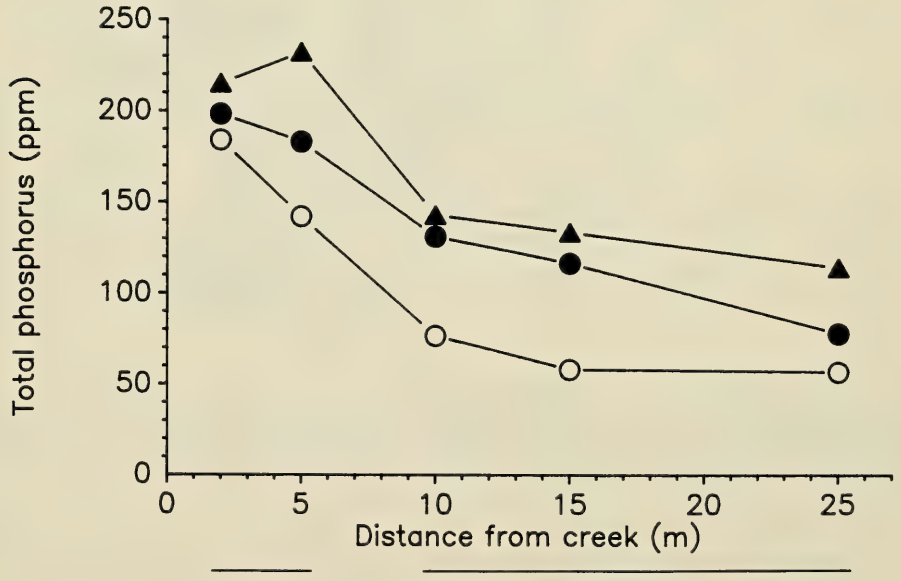

Fig. 3. The average total soil phosphorus of creek sites; O creek 1; • creek 2; ▲ creek 3. The solid lines below the x-axis indicate the groupings of phosphorus levels on distance from the creek determined by the SNK test ($\alpha = 0.05$).

defined as the property edge at developed boundaries and as the ridgetop edge at undeveloped boundaries. The slope of each transect was measured.

Section Four

Soil was sampled below stormwater outlets located in valley systems 1,3 and 7 (Fig. 1), where the surrounding development was at least 30 years old. Samples were collected from 2m, 10m and 30m downslope of the outlet, and 5m and 15m across slope from the outlet at a level 10m below the outlet. Soil samples were collected from sites adjacent to sewerage lines in valley 1 which were constructed in 1973 and ran downslope from the property boundary to the creek. Three samples were collected from directly overlying the sewerage line (located at least 30m apart) and one each from 5m and 10m across slope from the sewerage line. Soil was also sampled from sites adjacent to roads without kerb and guttering which were at least 20 years old, from valley systems 6 and 8 (Fig. 1). Two samples from each of 2m and 10m from the road and one from 30m, were collected from both upslope and downslope locations. There were four replications for each point source.

For sections two, three and four, each sampling site was located at least 50m across slope from any other possible nutrient source. The exception was section four, where stormwater outlets cannot be separated from the suburban boundary.

Soil Sampling and Analysis

At each site five soil cores in a grid of $5m^2$ (section one) or $1m^2$ (sections two, three and four) were sampled. Surface litter was removed and each soil core was collected using an auger of 25mm width and 75mm depth. The five soil cores were than bulked, air-dried and passed through a 2mm sieve to remove stones and litter before laboratory analysis. The samples were analysed for total soil phosphorus following the method of Lambert (1982).

Results

Samples and Analysis

Section One

There was a significant difference in total soil phosphorus between the five site types sampled ($F=10.7$, $df=30,4$, $P<0.001$) (Fig. 2). Undeveloped ridgetop sites and associated hillslope sites below, and hillslope sites downslope of suburban development, had soil phosphorus levels in the range of 30-100 ppm, with a mean value of 63 ppm. Suburban boundary sites showed significantly higher phosphorus levels, with a mean value of 135 ppm, and creek sites were higher again with a mean value of 186 ppm.

Section Two

Analysis of variance showed that total soil phosphorus differed significantly with distance from the creek bank ($F=16.71$, $df=4,29$, $P<0.001$) and among individual creeks ($F=10.7$, $df=2,29$, $P<0.001$). Sites closest to the creek bank (2m and 5m) had significantly higher phosphorus levels than sites located 10m, 15m and 20m from the creek bank (Fig. 3). Soil phosphorus levels at creek two sites were consistently higher than at creek one sites, and levels at creek three sites were consistently higher than at creek two. This could be due to a number of factors such as ratio of developed catchment to valley area, volume of water flow, flood discharge and sediment load. Only information on the ratio of developed catchment to valley area is known, and the differences between these ratios do reflect differences in soil phosphorus between the creeks (creek one, 3.4; creek two, 7.2; creek three, 12.3 (Buchanan 1983)).

Section Three

Sites adjacent to suburban boundaries were found to differ significantly in soil phosphorus levels with age of surrounding development ($F=21.14$, $df=2,29$, $P<0.001$) and with distance from the boundary ($F=5.05$, $df=4,29$, $P<0.01$). Sites adjacent to undeveloped ridgetops had significantly lower soil phosphorus levels than sites adjacent to suburban development (mean value 56 ppm and 83 ppm respectively) (Fig. 4). Although sites adjacent to development 35 years old had generally higher soil phosphorus levels than sites adjacent to 15 year old development, this difference was not significant.

Soils sampled at different distances from the undeveloped boundary showed no significant difference in phosphorus level (t-test: $p>0.05$, $df=6$). In contrast, soils within 20m of the suburban boundary had significantly higher phosphorus levels than soils 20m to 40m from the boundary (mean value 90 ppm and 73 ppm respectively) (t-test: $p>0.05$, $df=38$).

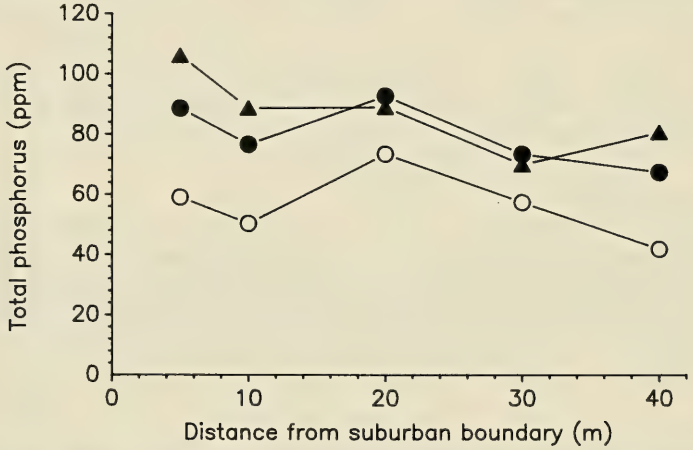

Fig. 4. The average total soil phosphorus of sites adjacent to suburban boundaries; O no development; • development since 1970; ▲ development since 1950.

Section Four

Sites below stormwater outlets showed no difference in soil phosphorus levels among the spatial sites below each outlet ($F=2.7$, $df=4,12$, $P>0.1$), although there was a significant difference in soil phosphorus among individual outlets ($F=26.7$, $df=3,12$, $P<0.001$). The mean soil phosphorus content of soils below the stormwater outlets was 438 ppm. This is 4-5 times higher than the levels associated with the edge of suburban development and 6 times higher than the levels for hillslope sites of the same suburban valleys. As phosphorus levels for sites located 50m across slope from stormwater outlets in previous sections were significantly lower than levels for sites located only 15m across slope, the affected area can be estimated to between 30m and 100m wide and extending at least 40m downslope from each outlet. Soils overlying sewerage lines had significantly higher phosphorus contents than soils 5m and 10m across slope (mean value 113 ppm and 70 ppm respectively) (Fig. 5**a**). Total phosphorus was found to be significantly higher for soils downslope compared to upslope of roads ($F=8.35$, $df=1,18$, $P<0.01$) and for soils less than 10m compared to greater than 10m from the road edge ($F=3.99$, $df=2,17$, $P<0.05$) (Fig. 5**b**). There was no significant difference in phosphorus level among upslope sites (t-test: $P>0.05$, $df=5$). However, sites 2m downslope of the road had significantly higher phosphorus levels than sites 10m and 30m downslope (575 ppm and 163 ppm respectively).

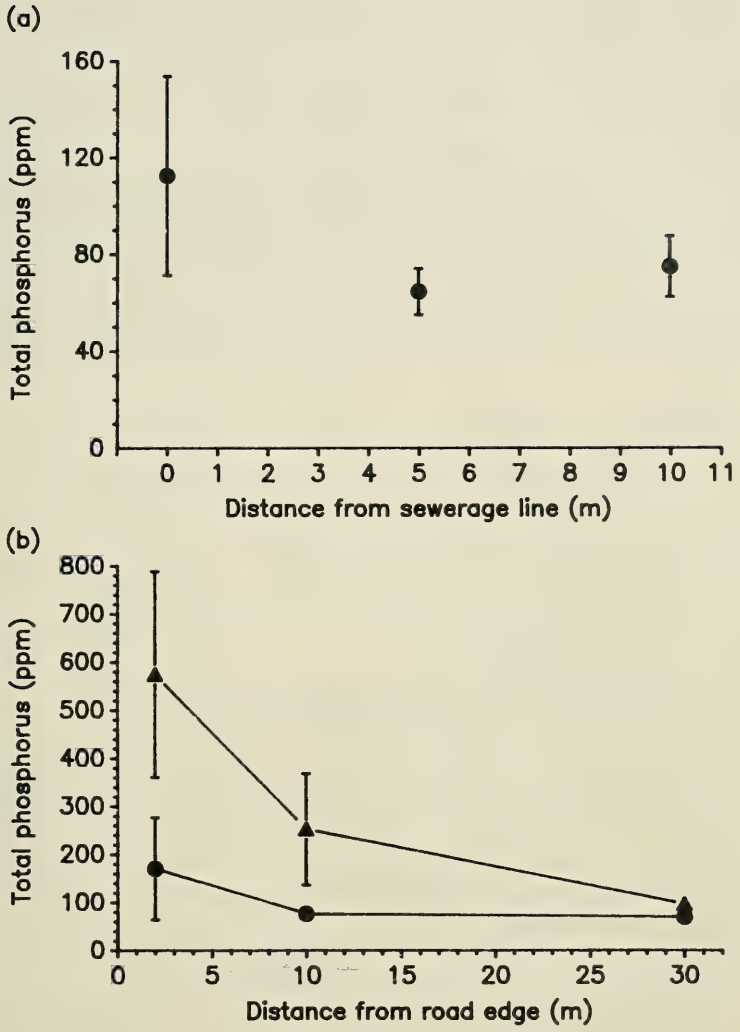

Fig. 5. The average total soil phosphorus of (**a**) sewerage line sites and (**b**) road sites; ▲ downslope of roads; ● upslope of roads. The error bar shows standard deviation.

Discussion

The results clearly show that there is an increase in total soil phosphorus within urban bushland areas. There is evidence for local enhancement of soil phosphorus levels, associated with particular nutrient sources, with the level of enhancement depending on both the nature and location of the source.

Sites adjacent to creeks and suburban boundaries were found to be areas of significant phosphorus enhancement. Nutrient input to creeks would come mainly from stormwater runoff and sewage overflows during heavy rainfall. The area of enhancement adjacent to creeks is confined to within 5m of the creek bank, with phosphorus levels within this area approaching 200 ppm. This is considerably higher than for comparable sites in non-suburban bushland. For example, Beadle (1962) found average soil

phosphorus levels of 98 ppm in Hawkesbury Sandstone valleys supporting depauperate rainforest. The abrupt change in phosphorus levels between sites 5m and 10m from the creek bank suggests that overbank deposits rather than downslope movement of soil materials are responsible for the increased levels. Observations of flood debris confirm that the area of enhancement corresponds roughly with the zone flooded during heavy runoff events.

There are a number of possible sources of phosphorus associated with the suburban boundary. These include runoff from properties (containing sediment, fertilizers, pesticides, *etc*) and dumped garden rubbish. The relatively small increase in phosphorus levels of these sites, irrespective of age of surrounding development, suggests that these sources contribute only a small amount of additional nutrient to urban bushland. However the location of suburban development on the ridges above bushland areas results in considerable downslope movement of these nutrients. Consequently the area of enhancement extends 20m below the suburban boundary, despite the low level of enhancement.

The topographic location of nutrient sources in urban bushland is critically important in determining the extent of the spread of phosphorus away from the source. Soils downslope of roads, stormwater outlets and suburban boundaries show phosphorus enhancement over a large area. In contrast, soils upslope or across-slope from sources such as creeks, roads and areas of introduced fill, show only a limited area of enhancement. Several studies (Bliss *et al.*, 1983; Wright, 1984) have shown that 80-90% of the total phosphorus in urban runoff is associated with particulates. Thus the movement of phosphorus is associated directly with the movement of soil and plant particles rather than in solution with groundwater.

The largest areas and highest levels of phosphorus enhancement in urban bushland were found to be associated with roads and stormwater outlets. Soil phosphorus levels adjacent to these sources were approximately five times that of suburban hillslope sites (Fig. 6). The area of enhancement downslope of roads and stormwater outlets extended up to 30m and at least 40m respectively from the source. The main contributor of nutrients to these sources is stormwater runoff. This runoff enters bushland via creeks, off paved surfaces such as roads and through stormwater outlets. Most areas of urban bushland have several stormwater outlets located at their boundary and stormwater is released directly onto the hillslope below. Sites subject to stormwater runoff (e.g. creeks, downslope of roads and stormwater outlets) had greatly enhanced levels of soil phosphorus compared to both suburban hillslope sites and sites adjacent to other nutrient sources such as introduced fill (e.g. sewerage lines, immediately upslope of roads) and dumped garden rubbish (e.g. suburban boundary) (Fig. 6). It is obvious that the major source of nutrient enrichment in urban bushland is urban runoff. In unsewered areas, stormwater runoff would be expected to carry an even higher nutrient load.

All sites sampled which had increased levels of soil phosphorus were associated with the presence of weed species. These weed species were not found in areas remote (e.g. more than 100m) from nutrient sources. Several authors have also reported the presence of weed species adjacent to nutrient sources. Buchanan (1983) reported the presence of a band of weeds 2m–5m wide and of moderate intensity along creeks and a weed band associated with the urban boundary of 5m–10m. She also reported dense weeds downslope of road batters consisting of clayey fill while upslope is weed-free. Plumes of weeds downslope of stormwater outlets have been recorded by Buchanan (1983) and Wright (1984).

A simple causal relationship between nutrient sources and the presence of exotic species cannot be assumed. Several factors need to be considered such as the type of exotic species present and other possible forms of disturbance. This is illustrated in

Table 1 where qualitative observations on factors of disturbance and the presence of exotic species at different locations within urban bushland are systemized. Examination of Table 1 shows that an increase in soil phosphorus is usually associated with an increase in soil moisture. Locations where both these forms of disturbance are present are characterized by the presence of weed species such as *Ligustrum sinense* (Small-leaved Privet), *Tradescantia albiflora* (Wandering Jew), *Ipomoea indica* (Morning Glory), *Cardiospermum grandiflorum* (Balloon Vine) and *Lonicera japonica* (Japanese Honeysuckle). In contrast, in areas where mechanical disturbance of the soil and canopy loss are the important factors of disturbance, species such as *Pennisetum clandestinum* (Kikuyu), *Cortaderia selloana* (Pampas Grass), *Rubus vulgaris* (Blackberry), *Eupatorium adenophorum* (Crofton Weed) and *Lantana camara* (Lantana) are found. Thus the addition of nutrient in the form of phosphorus appears to be an important factor in the establishment of weed species in urban bushland areas. When phosphorus addition is combined with other factors of disturbance then weed invasion may result.

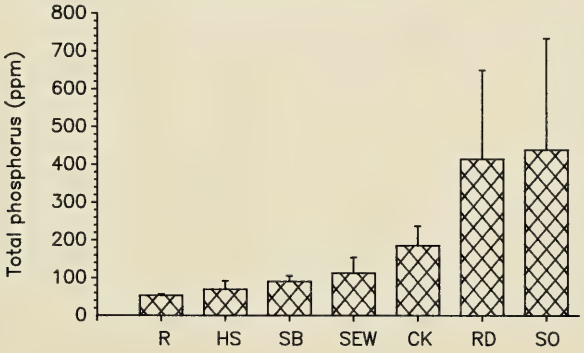

Fig. 6. The average total soil phosphorus levels of all site types sampled; R undeveloped ridgetop; HS hillslope; SB suburban boundary; SEW sewerage line; CK creek; RD road; SO stormwater outlet. The error bar shows standard deviation.

This study has clearly demonstrated elevated levels of soil phosphorus adjacent to nutrient sources within urban bushland. Clements (1983) suggests that a general enrichment of nutrient levels of urban bushland soils also has occurred. However the large natural variation in nutrient levels within the Hawkesbury Association soils, due to interbedding of shale and proximity to the Wianamatta Shale boundary, makes this conclusion doubtful without further sampling. I suggest that in small (*ie* less than 10 ha) bushland areas, a general increase in soil phosphorus levels is likely as affected areas (*ie* those downslope of nutrient sources such as stormwater outlets) expand and coalesce. However in larger bushland areas, where the affected areas are small relative to the total size, soil phosphorus levels will increase only very slowly as soil particle movement and nutrient recycling redistribute the nutrients within the system. Consequently the problem areas of weed invasion will remain confined to soils adjacent to nutrient sources. The most important consequence of this for managers of urban bushland is that reduction of nutrient and sediment loads of stormwater runoff and the control of stormwater release must be a major priority.

TABLE 1

A comparison of factors of disturbance with exotic species present at five locations within urban bushland. Disturbance factors, level of infestation and presence of exotic species are ranked according to total soil phosphorus as determined in this study for nutrient, general knowledge for other disturbance factors and qualitative field notes taken during this study for level of infestation and presence of exotic species. Ranks are from 1 to 5 representing least to most important. Plant nomenclature follows Beadle et al *(1982).*

	LOCATION				
	Suburban Boundary	**Sewerage Line**	**Creek**	**Road**	**Stormwater Outlet**
FACTOR OF DISTURBANCE					
Nutrient	1	1	3	4	5
Moisture	1	1	5	3	4
Soil Turnover	3	5	1	4	2
Canopy Loss	4	3	1	5	2
LEVEL OF INFESTATION	2	1	3	4	5
EXOTIC SPECIES PRESENT					
Ligustrum sinense *Tradescantia albiflora*	2	1	5	3	4
Pennisetum clandestinum *Cortaderia selloana*	4	5	1	3	2
Rubus vulgaris *Lantana camara* *Eupatorium adenophorum*	4	5	2	3	1
Ipomoea indica *Cardiospermum grandiflorum* *Lonicera japonica*	2	1	3	4	5

ACKNOWLEDGEMENTS

I would like to thank Mark Westoby for his advice and encouragement throughout this project; also M. Lambert and the staff of the Chemistry Division, N.S.W. Forestry Commission for use of a soil sampler and equipment for the analyses; and staff of the Engineering and Parks Department of Ku-ring-gai Municipal Council for the provision of maps and for general advice.

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Psocoptera (Insecta) from Nest Webs of *Badumna candida* (L. Koch) (Desidae: Araneae) in Queensland

C. N. SMITHERS

SMITHERS, C. N. Psocoptera (Insecta) from nest webs of *Badumna candida* (L. Koch) (Desidae: Araneae) in Queensland. *Proc. Linn. Soc. N.S.W.* 112 (1), 1990: 27-31.

Two new species of Psocoptera are described and records of another five species from the nest webs of the spider *Badumna candida* (L. Koch) are given from Townsville, Queensland. Most of the species are usually inhabitants of dried leaves, material which the spiders incorporate into their nest webs.

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KEY WORDS: Psocoptera, Ectopsocidae, Liposcelidae, Pseudocaeciliidae, *Badumna*, *candida*, Desidae, Queensland.

INTRODUCTION

New (1974) recorded ten species of Psocoptera (Insecta) from the nests of the spider *Badumna candida* (L. Koch) (as *Ixeuticus candidus* (L. Koch)) in Victoria. During studies of the nest webs of the same species of spider at Townsville, Queensland, M. F. Downes has taken several species of Psocoptera, some of which represent two undescribed species. This material is recorded here. Further details of their occurrence in association with the spiders will be published elsewhere by Downes.

NEW SPECIES AND NEW RECORDS

LIPOSCELIDAE

Liposcelis spp.

The collection contains a few specimens of *Liposcelis* (2 spp.) which cannot be identified until further work has been done on the Australian members of this large genus, some species of which are worldwide in distribution.

ECTOPSOCIDAE

Ectopsocus downesi sp.nov.

FEMALE

Coloration (in alcohol). Head and antennae pale brown with faintest suggestion of darker epicranial patches. Fourth segment of maxillary palp a little darker than head. Body and legs pale brown. Fore wings (Fig. 1) very faintly tinged with brown, the shading paler adjacent to veins, darker at ends of main veins and at Rs and M junction. Hind wing (Fig. 2) hyaline.

Morphology. Length of body: 1.6mm. Median epicranial suture indistinct. Head strongly setose except for glabrous genae. Lengths of flagellar segments: fl:.11mm; f2:.07mm. Antennae short, reaching only to about base of abdomen. Eyes fairly small, not reaching level of vertex. IO/D (Badonnel): 2.6; PO:.66. Median ocellus much smaller than lateral ocelli. Femora of all legs a little broader than usual in the genus, clearly much broader than tibiae. Hind femur about three times as broad as tibia, broadest at distal quarter. Measurements of hind leg: F:.27mm; T:.41mm; t1:.12mm; t2:.06mm; rt:2:1; ct:10,0. Fore wing length: 1.13mm; width: .46mm. Fore wing (Fig. 1)

broad and rounded distally. Pterostigma slightly convex behind, as wide as costal cell. Rs and M meet in a point. Wing margin setose from base of costa to nodulus, hind margin glabrous from nodulus to wing base. Wing setae very strong, especially so in basal half of wing. Wing margin with single row of setae except from base of pterostigma to about R4+5, where there is a double row. Hind wing (Fig. 2) glabrous except for strong marginal setae between R2+3 and R4+5. Epiproct lightly sclerotized with two strong setae on posterior margin, two strong setae arising from body of epiproct as well as a small number of almost symmetrically arranged small setae. Paraproct (Fig. 3) with a field of eight trichobothria behind which is a row of fine setae. Hind margin with a large seta, one stout cone and a smaller one subtended by a small seta, near which is a smaller seta. Subgenital plate (Fig. 4) with well sclerotized, median posterior lobe with strong setae on each side of which the plate margin is very strongly sclerotized. Middle part of lobe lightly sclerotized. Body of plate clothed with fine setae. Inner side of plate ornamented medially with sinuous wrinkles and a reticulate pattern postero-laterally. Gonapophyses (Fig. 5) with well sclerotized, pointed, ventral valve. Dorsal valve membranous, broad basally, curved and narrow distally, supported by a sclerotized bar in distal half. External valve long, narrow, broadest distally, with a few long apical setae of which one is clearly longer than the others. Dorsal border of valve heavily sclerotized, especially near base.

MALE Unknown.

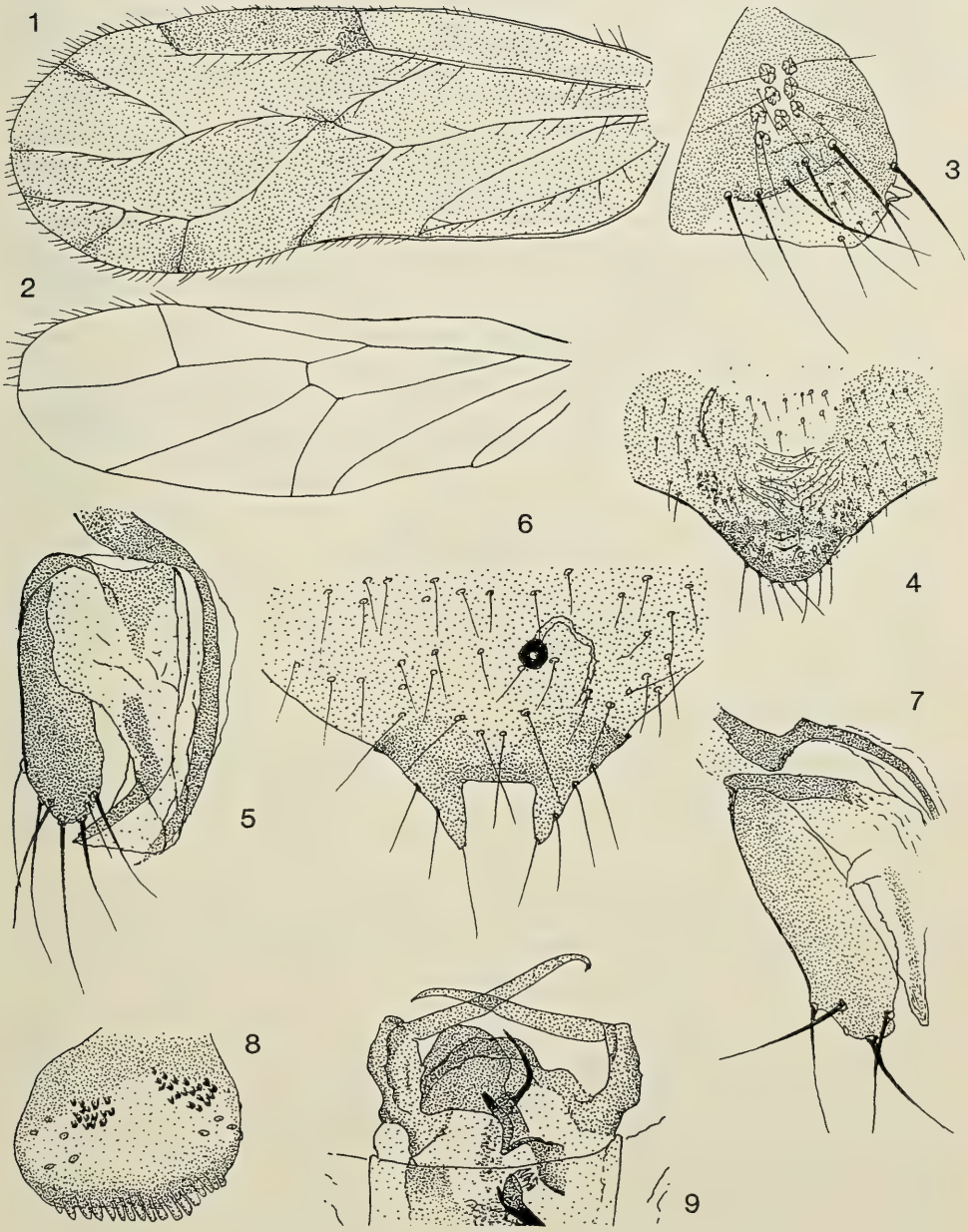
MATERIAL EXAMINED. Queensland. 1 female (holotype), from web of *Badumna candida*, Townsville, 2.ii.1987, M. F. Downes. 1 female (paratype), same data, 23.v.1988. Holotype and paratype in the Australian Museum.

DISCUSSION. *Ectopsocus downesi* belongs to the *E. hirsutus* group of species as defined by Thornton and Wong (1968, p. 145). It differs from *E. hirsutus* in having fewer setae on the external valve of the gonapophyses, one at the apex being stronger than the others. The hind margin of the apical lobe of the subgenital plate is not sinuous but smoothly rounded and the lobe is much more lightly sclerotized in the central part than *E. hirsutus*. The inner lining of the subgenital plate has a central area of sinuous lines flanked by an area of polygonal sculpturation on each side. This structure appears to be absent from other species of the group (cf. Thornton, 1962, fig. 36) except for *E. hirsutus* itself in which it has a different form. From *E. pilosus* Badonnel and *E. crinitus* Thornton and Wong *E. downesi* differs in the rounded hind margin of the posterior lobe of the subgenital plate and in those species the ventral valve is spiculate in the basal part. These spicules are not present in *E. downesi*. The subgenital plate resembles that of *E. thysanus* Thornton and Wong and *E. villosus* Thornton and Wong in that they all have a smoothly rounded hind margin bearing about eight strong setae. In *E. thysanus*, however, the lobe is evenly sclerotized and the hind margin of the plate lacks the strongly sclerotized margin lateral to the lobe. This is very strongly developed in *E. downesi*. In *E. downesi* the dorsal valve of the gonapophyses is apically narrow whereas in *E. thysanus* it is broad and membranous, apparently without any strengthening, longitudinal sclerotized band (Thornton and Wong, 1968, fig. 227). In *E. downesi* the ventral valve is much more strongly sclerotized than in *E. villosus* and *E. thysanus*. In *E. boharti* Thornton and Wong the posterior lobe of the subgenital plate is not clearly marked off from the body of the plate nor is it more heavily sclerotized. The dorsal valve of the gonapophyses has an accessory lobe and is not supported by a sclerotized bar.

Ectopsocus unipunctatus sp.nov.

FEMALE

Coloration (in alcohol). Head and appendages almost uniformly pale brown but



Figs. 1-9. Ectopsocus downesi sp.nov. **1.** Fore wing, female. **2.** Hind wing, female. **3.** Paraproct, female. **4.** Subgenital plate, female. **5.** Gonapophyses, female. *Ectopsocus unipunctatus* sp.nov. **6.** Subgenital plate, female. **7.** Gonapophyses, female. **8.** Posterior abdominal tergum, male. **9.** Phallosome, male.

fourth segment of maxillary palp a little darker and abdomen has suggestion of lateral segmentally arranged marks. A tiny but very distinct black spot clearly visible on subgenital plate a little to left of midline. (This is part of the sclerotization of the 9th sternite which shows through the plate). Fore wings hyaline with faintest suggestion of brown tinge to membrane. Hind wings hyaline.

Morphology. Length of body: 1.7mm. Median epicranial suture indistinct. Head, except for glabrous genae, with scattered strong setae. Length of first flagellar segment: f1:.19mm. Base of first flagellar segment slightly enlarged. Eyes moderately large. IO/D (Badonnel):2.3; PO:.8. Measurements of hind leg: F:.32mm; T:.55mm; t1:.2mm; t2:.08mm; rt:2.5; ct:16,0. Fore wing length: 1.4mm; width: .51mm. Fore wing with Rs and M meeting in a point. Stem of Rs about half as long as R4+5. Stigmapophysis very prominent. Veins, except glabrous Cu2, with short setae. Margin glabrous. Hind wing with short crossvein between Rs and M; glabrous. Epiproct simply rounded behind, well sclerotized except for a lightly sclerotized ovoid apical area. Hind border with two long, strong setae arising from the margin in the lightly sclerotized area with another pair, one on either side, arising from the more heavily sclerotized area. A few smaller setae arise from the lightly sclerotized area. There is a transverse row of four setae across middle of epiproct with a second row of four between the first row and its base. Epiproct very similar to that of *E. vilhenai* Badonnel (cf. Badonnel, 1955, fig. 429) but with fewer setae in basal half. Paraproct with double cone on hind margin adjacent to which is a small seta with a large marginal seta dorsal to cone. Field of eight trichobothria and one seta without basal 'rosette' very similar to that of *E. vilhenai* (cf. Badonnel, 1955, figs. 430, 431). Subgenital plate (Fig. 6) with a pair of posterior lobes, lacking terminal hyaline extension but each with a terminal seta in addition to two or three lateral marginal setae. Border of subgenital plate between posterior lobes transverse. Gonapophyses (Fig. 7) with basal attachment of ventral and external valves very well sclerotized (visible as sinuous lines at low magnification). Dorsal valve membranous. Sclerification of 9th sternite (Fig. 6) in form of a small, very strongly sclerotized ring.

MALE

Coloration (in alcohol). As in female.

Morphology. General morphology of head as in female. Eyes larger than in female, just reaching level of vertex. IO/D (Badonnel):2.2; P0:.6. Length of flagellar segments: f1:.19mm; f2:.09mm. Measurements of hind leg: F:.32mm; T:.57mm; t1:.2mm; t2:.09mm; rt:2.2:1; ct:16,0. Fore wing length: 1.35mm; width: .21mm. Fore wing venation as in female but Rs stem about two thirds length of R4+5. Epiproct simple, with a few long, posterior setae. Hypandrium with sclerotized spur-like structure. Phallosome (Fig. 9) very large, complex, with long tongue-like structure arising near base and extending posteriorly. Posterior abdominal tergum (Fig. 8) (a little distorted in preparation) with a pair of rugose areas and a posterior comb.

MATERIAL EXAMINED. Queensland. 1 female (holotype), 2 males (including allotype), from web of *Badumna candida*, Townsville, 31.v.1988, M. F. Downes. 2 females (paratypes), same data, 18.iv.1988. Holotype, allotype and paratypes in Australian Museum.

DISCUSSION. *Ectopsocus unipunctatus* belongs to the *E. cinctus* group as defined by Thornton and Wong (1968, p.142). It is closest to *E. vilhenai*, which was described from Angola and has since been recorded from Madagascar and Reunion, Senegal, Nigeria, Jamaica, Trinidad, Mexico, Cuba, Marie Galante, Guadaloupe and Venezuela. Males of *E. unipunctatus* differ from those of *E. vilhenai* in the details of the distal part of the phallosome (cf. Badonnel, 1955, fig. 425) and in the structure of the posterior abdominal tergum (Badonnel, 1955, fig. 426). In particular, the posterior margin of the fused internal parameres is not sinuous as in *E. vilhenai* and the external parameres are almost straight, gradually tapering and curved at the ends. They are large enough to overlap

considerably in the midline. In *E. vilhenai* they are sinuous and much shorter, barely meeting in the midline. The anterior half of the phallosome is very similar to that of *E. vilhenai* which has a similar basal sclerite and spatulate posteriorly projecting flap (Badonnel, 1955, fig. 424). On the posterior abdominal tergum the arrangement and extent of the rugose areas are different, being less compact and less extensive in *E. unipunctatus* than in *E. vilhenai*. The female of *E. unipunctatus* lacks the apical extension to the posterior lobes of the subgenital plate (cf. Badonnel, 1955, fig. 427) and appears to lack a median rugose area on the subgenital plate basad of the posterior lobes.

Ectopsocus baliosus Thornton and Wong

MATERIAL EXAMINED. Queensland. 1 male, 1 female, from web of *Badumna candida*, Townsville, 6.v.1988, M. F. Downes. 1 female, same data, 14.iii.1988. 1 male, same data, 27.iv.1988, M. F. Downes.

E. baliosus was described from Malaya and subsequently recorded from Queensland, Reunion and Indonesia.

Ectopsocus russulus Smithers

MATERIAL EXAMINED. Queensland. 1 female, from web of *Badumna candida*, Townsville, 25.vi.1988. M. F. Downes.

E. russulus was described from Muogamarra Nature Reserve, near Sydney. This is the first subsequent record for the species.

PSEUDOCAECILIIDAE

Cladioneura foliata Smithers

MATERIAL EXAMINED. Queensland. 1 female, from web of *Badumna candida*, Townsville, 18.iv.1988. M. F. Downes. 1 female, same data, 28.i.1988, M. F. Downes.

Cladioneura foliata was described from Barrow Island, Western Australia. This is the first subsequent record for the species. In the two specimens from Queensland one has a definite crossvein between Rs and M in the fore wing and in the other, a much paler specimen, these two veins meet in a point as in the male type. The Queensland specimens are also a little larger than those from Barrow Island. The species is clearly somewhat variable in depth of colour pattern and details of venation. The present specimens agree well with the Barrow Island material in features of the genitalia.

Acknowledgements

I would like to thank Mr. Downes for the opportunity of studying his material and Dr. Gray for comments on the nomenclature of the spider species from the nests of which the material was collected.

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Calcium Borosilicate Minerals from Devils Elbow, Nundle Area, New South Wales

P. M. ASHLEY

(Communicated by B. E. CHENHALL)

ASHLEY, P. M. Calcium borosilicate minerals from Devils Elbow, Nundle area, New South Wales. *Proc. Linn. Soc. N.S.W.* 112 (1), 1990: 33-46.

The relatively uncommon borosilicate minerals, datolite and axinite, occur in a vein paragenesis at Devils Elbow, near Nundle, northeastern New South Wales. Their paragenesis is a typical one, being within low-grade metamorphosed mafic rocks, limestone, cherty and volcaniclastic sediments of the Devonian Tamworth Group. Datolite is near stoichiometric in composition and is restricted to recrystallized limestone and cherty calcareous siltstone. Axinite is shown to be Fe-rich (ferroaxinite) and occurs in mafic rocks and volcaniclastic sandstone; host rock composition has influenced borosilicate mineral speciation. Vein formation has been attended by introduction of SiO_2, B_2O_3 and minor As, and, from fluid inclusion data, is estimated to have occurred at 230°C-280°C, at pressures approximating 1kb and from dilute NaCl fluids. Hydrothermal fluids are similar to those responsible for the formation of extensive Au-Sb-W-As-bearing veins in the Nundle district. Borosilicate veining cuts metamorphic assemblages in Tamworth Group rocks which are tentatively favoured to be the result of contact metamorphism by the subjacent Permian Duncans Creek Trondhjemite. Vein formation may be no older than late Permian and coeval with the Nundle Au-Sb-W-As vein mineralization event. Indeed, borosilicate veining is probably a continuum from the latter, with the boron possibly derived from marine sediments and mafic rocks previously enriched in the element by spilitization reactions.

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INTRODUCTION

The calcium borosilicate minerals have typical parageneses in skarns and calcsilicate rocks where boron metasomatism has occurred and as veins and replacements in low-temperature metamorphosed mafic igneous rocks (e.g. Deer *et al.*, 1962, 1986; Vallance, 1966). In these occurrences, they are associated with other calcsilicate minerals, tourmaline, calcite, quartz, fluorite, chlorite and albite.

In this paper, a vein paragenesis of datolite and axinite in limestone, mafic igneous rocks and clastic sediments is reported. During recent road widening operations, new exposures of vein minerals were afforded at Devils Elbow, 4km east-southeast of Nundle in northeastern New South Wales (Australian Map Grid Reference 9135-262161). Subsequent petrographic and electron microprobe examination confirmed the borosilicate phases. The location (Fig. 1) is within rocks assigned to the Silver Gully Formation of the Tamworth Group (Glenton, 1979; Ashley and Hartshorn, 1988) and is one of a number of axinite-bearing occurrences reported from the Nundle district. Benson (1913, 1915) was the first to report axinite, in association with quartz, epidote and calcite, in veins and vesicle fillings in mafic rocks of the Tamworth Group. Further occurrences were noted by Vallance (1960) and Glenton (1979) and the writer has found the mineral, with quartz and epidote, at a number of locations (e.g. G.R. 252258 and 264152) within mafic rocks of the Tamworth Group and Woolomin Group. Although the comparatively rare mineral datolite has been found in Tamworth Group equivalent rocks at Bundook, west of Taree (Vallance, 1960), its presence in the Nundle district does not appear to have been noted in the literature.

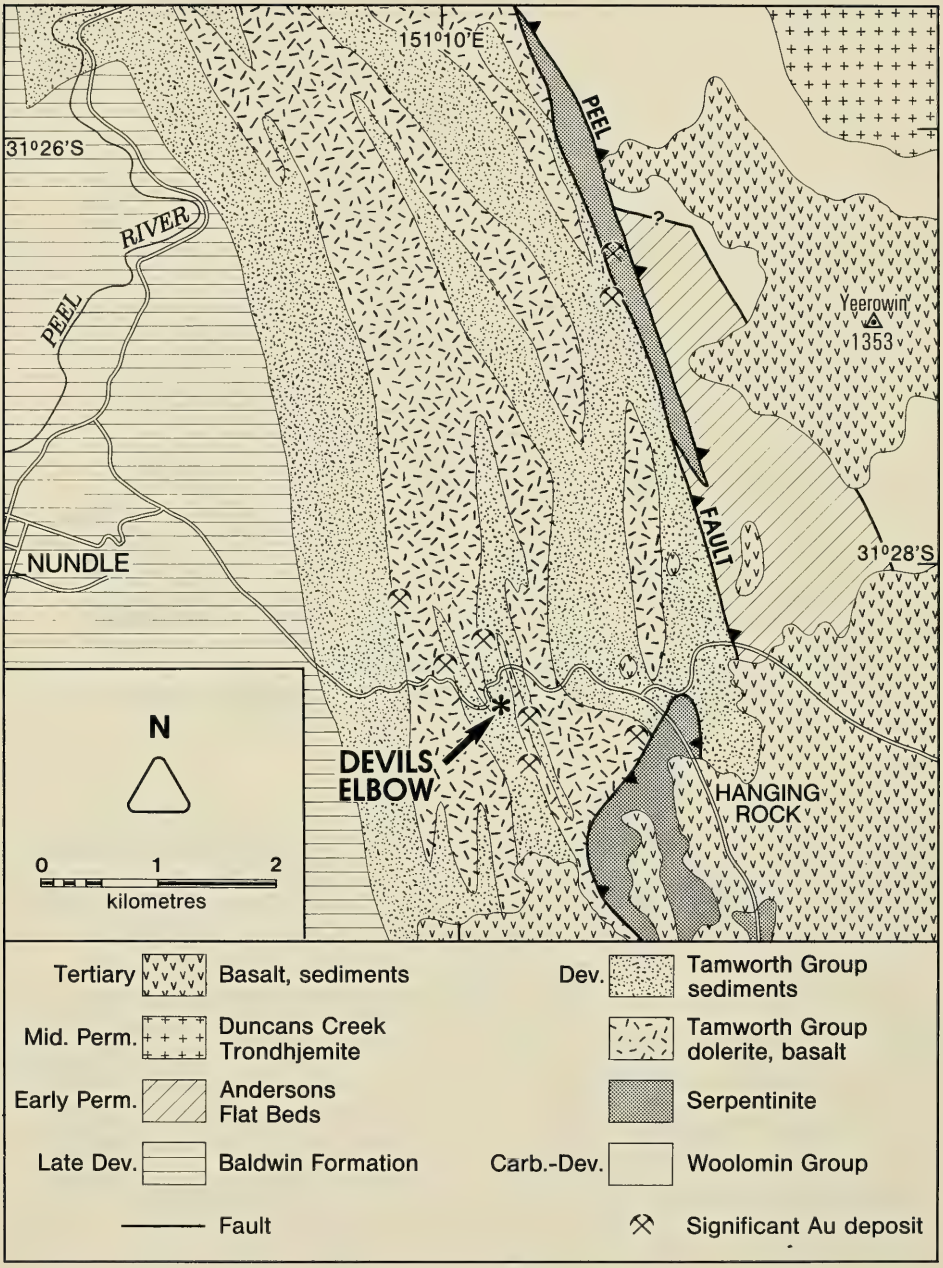

Fig. 1. Geology of the Nundle-Hanging Rock area, modified from Ashley and Hartshorn (1988), with location of Devils Elbow borosilicate mineral occurrence.

The Tamworth Group hosting the borosilicate minerals forms part of the Gamilaroi terrane of Flood and Aitchison (1988). It was deposited in the early to middle Devonian and consists of marine siltstone-argillite, volcaniclastic sandstone, spilitized mafic rocks (sills and flows), keratophyre, conglomerate and limestone (e.g. Benson, 1913, 1915; Vallance, 1960, 1969a, 1969b; Crook, 1961; Morris, 1988; Ashley and Hartshorn, 1988; Cawood and Flood, 1989). Recent interpretations favour the Tamworth Group to represent a dominantly volcaniclastic fore-arc sequence underlain by and intercalated with mafic igneous oceanic crustal rocks. The spilitized mafic rocks were favoured by Korsch (1977), Cross, (1983) and Morris(1988) to have developed as a result of rifting of the fore-arc basin, although Cawood and Flood (1989) suggest their generation in a magmatic arc. Tamworth Group rocks are bounded to the east by the Peel Fault, along which elements of the Great Serpentinite Belt (Weraerai terrane of Flood and Aitchison, 1988) have been emplaced. The Peel Fault separates the Tamworth Group from the Woolomin Group and Andersons Flat Beds (Djungati terrane of Flood and Aitchison, 1988), with the Woolomin Group having been intruded by the Permian Duncans Creek Trondhjemite (Fig. 1).

Geological Setting and Petrography

At Devils Elbow, the Silver Gully Formation consists of low grade metamorphosed, well-bedded cherty calcareous siltstone grading to medium grained volcaniclastic sandstone, massive medium-grained dolerite and minor fine-grained basalt, and a distinctive recrystallized bioclastic limestone bed. There is commonly excellent preservation of primary sedimentary and igneous textures in the rocks and although the terms spilite and metabasite have been widely employed for the low grade mafic rocks of the Nundle district (e.g. Benson, 1915; Vallance, 1960, 1969b, 1974; Morris 1988; Cawood and Flood, 1989), use of pre-metamorphic rock terminology is preferred in this paper. The limestone bed was originally reported by Benson (1913) and informally termed Devils Elbow Limestone Member by Glenton (1979) and Pickett (1986). The sequence dips east-northeast at 70° and is probably overturned, based on district stratigraphic configuration. The dolerite may have intruded the limestone bed, as suggested by Benson (1913) and by a recently exposed prominent chilled margin on the sill-like mafic body. The limestone bed is approximately three metres thick, bounded to the west by dolerite and minor basalt, and to the east by siltstone and sandstone. Although recrystallized, the limestone contains a shelly and coralline fauna, and Pickett (1986) reported the presence of late early Devonian conodonts. Glenton (1979) suggested that the limestone has been redeposited and thus the fossil remains are not necessarily indicative of the age of the bed.

Vein assemblages occur in all lithologies but are most evident in limestone where they form steeply dipping, simple planar and anastomosing arrays up to 3cm wide which cut the stratigraphy at a high angle. Datolite-bearing veins occur in limestone (Fig. 2**a**) and siltstone whereas axinite-bearing assemblages appear to be restricted to the mafic igneous rocks (Fig. 2**b**) and volcaniclastic sandstone. The two borosilicate minerals have not been found together.

Datolite is found as pale brown and pale green to white aggregates in which squat barrel-shaped to prismatic grains attain a maximum grainsize of 3mm. Mostly, however, it forms a granular mosaic with a grainsize of <0.5mm. In the veins, the mineral is associated in apparent textural equilibrium with calcite and minor quartz, chlorite and prehnite. Datolite grains are unstrained, contain locally abundant fluid inclusions and have undergone slight intragranular retrogression to calcite. The latter is texturally distinct from the medium to coarse grained calcite coexisting in apparent

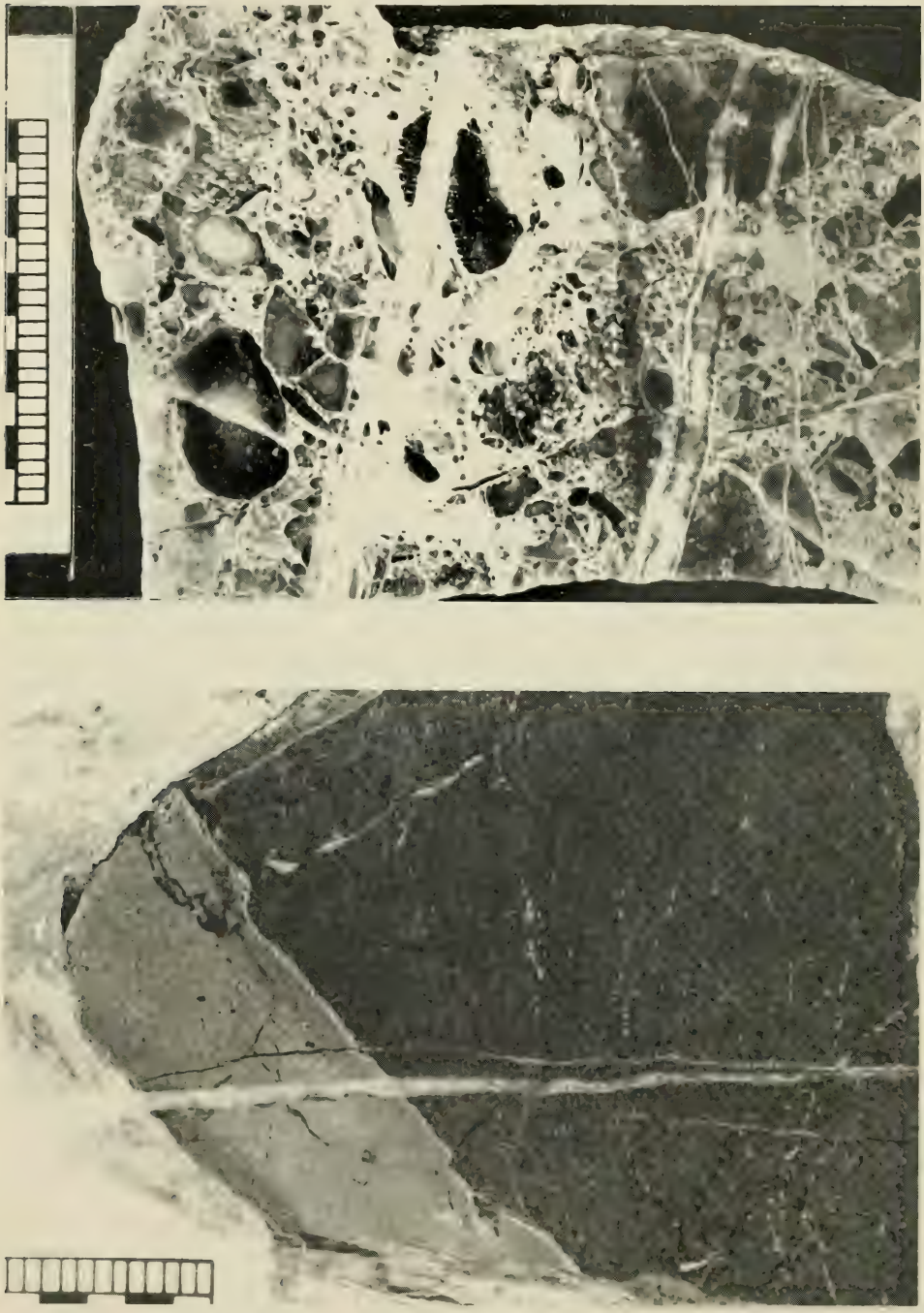

Fig. 2. **a.** Bioclastic limestone slab with fragments up to 4 cm across in a pale-coloured fine grained calcsilicate matrix and cut by planar datolite-quartz veins up to 7 mm wide. Scale is 5 cm long. Sample R63079, Devils Elbow. **b.** Slab showing contact between basalt (medium grey) and medium grained dolerite (dark grey) cut by planar axinite-quartz veins up to 8 mm wide. Scale is 2.5 cm long. Sample R63077, Devils Elbow.

equilibrium with datolite. Limestone in which datolite-bearing veins occur contains recrystallized calcite (commonly pseudomorphing bioclastic material) in a formerly calcareous muddy matrix now recrystallized to fine-grained aggregates of subhedral garnet and minor vesuvianite, diopside, clinozoisite, titanite (sphene), albite and apatite. Electron microprobe analyses of garnet show that it is grossular ($Gr_{93.4\text{-}95.2}Ad_{1.2\text{-}2.3}Al_{1.8\text{-}4.4}Sp_{0.1\text{-}0.2}Py_{0.6\text{-}0.8}$) and associated vesuvianite is relatively Mg-rich with a composition of $Ca_{9.1}Mg_{1.2}Fe_{0.8}Ti_{0.2}Al_{4.3}Si_{8.9}O_{34}(OH)_4$. The minor Fe in the rock is strongly partitioned into vesuvianite. Bedded siltstone hosting datolite-bearing veins contains volcaniclastic albitized plagioclase in a recrystallized cherty matrix studded with subradiating aggregates and prismatic grains of diopside and actinolite, plus minor titanite.

Axinite occurs as pale mauve prismatic grains up to 6mm long. Prisms are commonly aligned both parallel and normal to vein walls. Accompanying vein minerals are quartz, calcite, minor chlorite and traces of sphalerite and pyrrhotite. Although epidote accompanies axinite in many veins in the Nundle district, the association has not been observed at Devils Elbow. Axinite shows faint mauve and blue pleochroism and is incipiently replaced by calcite. Dolerite, basalt and volcaniclastic sandstone hosting axinite-bearing veins retain relict textures, with primary clinopyroxene and magnetite; other minerals, however, are metamorphic and include albite, actinolite, chlorite, epidote with traces of titanite, pyrite, chalcopyrite, pyrrhotite, pumpellyite, carbonate and quartz. Pumpellyite appears to be largely restricted to former calcic plagioclase cores.

Chemistry of Borosilicate Minerals and Enclosing Rocks

Electron probe microanalysis was used to ascertain compositions of the borosilicate minerals but as boron was not able to be determined, the content of B_2O_3 (as well as H_2O) was calculated assuming stoichiometry. Datolite from the Devils Elbow veins proves to be close to $CaBSiO_4(OH)$ with analyses (Table 1) indicating insignificant substitution of other components. The results match other datolite analyses (e.g. Deer *et al.*, 1962) and the atomic Si:Ca ratio close to unity implies no substitution of the closely related bakerite $CaB_4BO_4(SiO_4)_3(OH)_3.H_2O$ molecule. Datolite coexists with essentially pure calcite in limestone and with minor ferrian prehnite and pycnochlorite (Table 1) in siltstone.

Axinites analysed from Devils Elbow are ferroaxinite in the classification of Sanero and Gottardi (1968), with Ca > 1.5 atoms per formula unit (pfu) and Fe > Mn (Table 1). Results from two samples show a considerable range in Mg, Fe and Mn contents with Mg being negatively correlated with Mn and Fe (Fig. 3). Consistent with other ferroaxinites, Ca is close to 2 atoms pfu, but the total Fe content of the mineral is particularly high, ranging toward the highest reported values (*cf.* Lumpkin and Ribbe, 1979; Deer *et al.*, 1986). Calcites coexisting with axinite include stoichiometric $CaCO_3$ in sample R63077 (University of New England, Department of Geology and Geophysics collection) and a manganoan variety $(Ca_{0.87}Mg_{0.02}Fe_{0.02}Mn_{0.09})CO_3$ in sample R63078. Associated chlorites are ripidolite (Table 1) which are richer in Fe and Mn than the pycnochlorites coexisting with datolite.

The fact that Ca borosilicate speciation and composition of associated minerals vary in different lithologies implies that bulk rock chemistry has influenced vein mineralogy, assuming that the vein fluids had relatively constant aB_2O_3. It is interpreted that datolite-bearing veins have formed in response to low Al, Fe, Mn and Mg contents of host limestone and siltstone, whereas the higher contents of these elements in mafic rocks and sandstone have resulted in the crystallization of axinite and relatively Fe-rich chlorite.

TABLE 1

Electron microprobe analyses of Devils Elbow borosilicate and associated vein minerals

	1	2	3	4	5	6	7	8
SiO_2	37.17	37.53	41.56	42.40	41.46	27.28	25.27	25.01
TiO_2			0.06	0.04	0.07			
Al_2O_3	0.03	0.02	18.15	18.65	21.71	19.18	19.49	19.11
B_2O_3*	21.76	21.76	6.20	6.22				
Cr_2O_3							0.04	
ΣFeO			8.91	7.73	4.16+	21.06	32.60	31.61
MnO			2.68	0.32		0.22	0.43	0.40
NiO						0.03		0.03
MgO			1.21	2.81		19.21	11.34	11.74
CaO	35.01	35.01	19.63	19.64	25.90	0.09	0.05	0.07
Na_2O		0.02	0.02					0.03
K_2O						0.01		
Total	93.97	94.34	98.42	97.81	93.30	87.08	89.22	88.00
	4.5(O)		31(O)		11(O)		28(O)	
B	1.003	1.000	2.023	2.005				
Si	0.994	1.000	7.859	7.922	2.964	5.657	5.460	5.463
Aliv	0.001		0.141	0.078	0.036	2.343	2.540	2.537
Alvi		0.001	3.904	4.031	1.797	2.344	2.420	2.382
Ti			0.009	0.006	0.004			
Cr							0.005	
ΣFe^{2+}			1.409	1.208	0.224+	3.653	5.890	5.775
Mn			0.430	0.051		0.039	0.078	0.073
Ni						0.005		0.005
Mg			0.341	0.783		5.937	3.651	3.821
Ca	1.003	0.999	3.977	3.932	1.984	0.019	0.011	0.016
Na		0.001	0.007					0.011
K						0.003		
Σ	3.003	3.001	20.100	20.016	7.009	20.000	20.055	20.083
mg			0.195	0.393		0.619	0.383	0.398

Analyst: P. M. Ashley. Cameca instrument, R.S.E.S., Australian National University, Canberra. Blank = below detection limit: Cr_2O_3 0.04%; FeO, MnO, NiO 0.03%; TiO_2, MgO, Na_2O 0.02%; K_2O 0.01%.
* B_2O_3 calculated. Total Fe as FeO, except in analysis 5 (+) where Fe is calculated as Fe_2O_3.

1. Datolite (average of 5 analyses) from datolite-ferrian prehnite-pycnochlorite-quartz vein in siltstone. Sample R63076.
2. Datolite (average of 6 analyses) from vein in limestone. Sample R63062.
3. Ferroaxinite (average of 7 analyses) from ferroaxinite-quartz-calcite-ripidolite vein in dolerite. Sample R63077.
4. Ferroaxinite (average of 4 analyses) from ferroaxinite-quartz-manganoan calcite-ripidolite vein in dolerite. Sample R63078.
5. Ferrian prehnite (average of 4 analyses) from analysis 1 assemblage. Sample R63076.
6. Pycnochlorite (average of 3 analyses) from analysis 1 assemblage. Sample R63076.
7. Ripidolite (average of 2 analyses) from analysis 4 assemblage. Sample R63078.
8. Ripidolite (average of 2 analyses) from analysis 3 assemblage. Sample R63077.

All samples in this paper are housed in the collection of the Department of Geology and Geophysics, University of New England.

Whole-rock chemical analyses have been carried out on two samples with conspicuous borosilicate veining and two on adjacent unveined material. Unveined limestone contains a relatively minor non-carbonate detrital component, expressed as SiO_2, Al_2O_3 and TiO_2 (Table 2). The B_2O_3 content (0.13%) is well above typical values for limestones (20 ppm B; Harder, 1974), perhaps implying at least local pervasive

introduction and permeation of B throughout the limestone. Datolite-veined limestone, in contrast, contains higher SiO_2, B_2O_3 and As (Table 2) suggesting addition of these components during vein formation. Small variations in other components are attributed to either primary heterogeneity in the limestone and/or dilution due to introduced material.

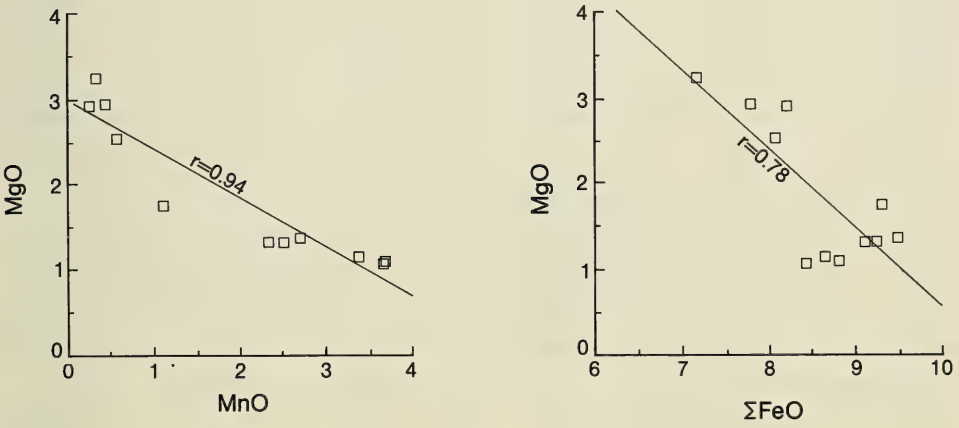

Fig. 3. Weight percent MgO versus MnO and total FeO in ferroaxinites from Devils Elbow.

Unveined dolerite from Devils Elbow is compositionally similar to other mafic igneous rocks from the Tamworth Group in the Nundle district (e.g. Vallance, 1974; Cross, 1983; Morris, 1988; Ashley and Hartshorn, 1988). The composition (Table 2) is consistent with mid-ocean ridge basalt (MORB) although one relatively enriched in TiO_2, total FeO/MgO, P_2O_5, Zr, Y and V, and relatively low in MgO, Ni and Cr (*cf.* Sun *et al.*, 1979). In comparison to fresh MORB (e.g. Melson *et al.*, 1976; Sun *et al.*, 1979), the Nundle rocks are richer in H_2O, Na_2O, K_2O, Rb and Sr. These are mobile components which may have been introduced by hydrothermal interaction with seawater or perhaps represent enrichments due to element redistribution via spilitic degradation during burial metamorphism. The fact that the Nundle dolerites have constantly high Na_2O (compared to MORB values) (*cf.* Morris, 1988; Ashley and Hartshorn, 1988) and that complimentary volumes of Na-depleted dolerite are not recognized, implies that Na and other enriched components have been added from a marine reservoir. Typical MORB basalt contains 2-8 ppm B (Humphris and Thompson, 1978; Seyfried *et al.*, 1984), although recent analyses by Spivack and Edmond (1987) of genuinely fresh MORB glasses yielded values of 0.2-0.4 ppm B. In any case, the value of 0.05% B_2O_3 in the unveined dolerite sample R63065 (Table 2) implies significant B addition. Such addition is logically from an ultimately marine source, as seawater contains on average 4.35 ppm B (e.g. Seyfried *et al.*, 1984) and that MORB-type basalts have been shown to be sinks for marine B during low and intermediate temperature hydrous alteration (Spivack and Edmond, 1987).

TABLE 2

Whole rock analyses of borosilicate-veined samples and adjacent rocks, Devils Elbow.

Sample	R63062	R63063	R63064	R63065	Av. TGM
SiO_2	15.03	6.07	52.92	50.20	49.41
TiO_2	0.14	0.11	2.02	2.19	2.22
Al_2O_3	2.01	1.55	14.23	13.41	13.85
Fe_2O_3	0.81	0.57	2.23	4.03	13.84*
FeO	0.34	0.31	6.24	8.83	
MnO	0.09	0.10	0.26	0.18	0.21
MgO	1.01	0.98	4.67	5.14	4.51
CaO	46.69	52.10	8.27	7.21	7.29
Na_2O	0.01	0.02	5.20	4.87	4.79
K_2O	0.07	0.04	0.51	0.74	0.39
P_2O_5	0.04	0.03	0.25	0.25	0.29
B_2O_3	5.26	0.13	0.78	0.05	
S	0.02	0.02	0.02	0.04	0.13
L.O.I.	28.91	37.97	2.35	2.43	2.87
less O=S	0.01	0.01	0.01	0.02	0.06
Total	100.42	99.99	99.94	99.55	99.74
			Trace elements ppm		
Li	<7	<7	7	11	
Ba	28	<5	93	158	74
Rb	2	1	6	10	5
Sr	147	184	211	347	235
U	2	3	<1	1	
Th	2	3	<1	<1	
Y	9	6	47	44	46
Zr	12	10	142	120	134
Nb	1	1	3	2	3
Ce	4	11	21	21	21
Nd	9	13	17	17	
La	5	2	5	5	8
Ga	5	3	16	15	20
Sc	<1	<1	43	47	38
V	24	12	405	546	407
Ni	6	6	26	24	22
Cr	42	24	48	32	21
Cu	16	16	6	13	47
Pb	<1	3	2	<1	<1
Zn	13	13	49	49	102
As	34	<1	32	5	4

Analysts: J. Bedford, J. Cook. Analyses by XRF except for FeO (titrimetry), L.O.I. (loss-on-ignition) (gravimetry), B_2O_3 and Li (ICP).

* Total Fe as Fe_2O_3. Blank = not determined.

R63062: Datolite-veined recrystallized limestone (containing minor grossular, vesuvianite and diopside).

R63063: Unveined recrystallized limestone with minor grossular, vesuvianite and diopside.

R63064: Axinite-veined dolerite.

R63065: Massive unveined dolerite.

Av TGM: Average of 30 Nundle area Tamworth Group dolerites and basalts from Ashley and Hartshorn (1988) (includes data from Morris, 1988).

Samples prefixed "R" from Australian Map Grid Reference 9135-262161.

In comparison to unveined material, dolerite with axinite-bearing veins is richer in SiO_2, B_2O_3 and As (Table 2) showing that the chemical changes are identical to those

operative in the formation of the datolite-veined limestone. Other minor chemical disparities may again be possibly attributed to primary heterogeneity and/or dilution effects.

Fluid Inclusions in Datolite-bearing Veins

Fluid inclusions are locally abundant in the vein minerals calcite, datolite, axinite and quartz. However, only in the datolite-bearing veins were they large enough (typically in the range 3-20μm across) to yield microthermometric data. The most suitable inclusions were found in a limestone-hosted, medium to coarse grained calcite-datolite vein in which the minerals appeared to be in textural equilibrium. Inclusions are primary and pseudosecondary types using the criteria of Roedder (1984), and show simple two-phase character with a constant liquid-to-vapour ratio of about 9:1. Those in calcite commonly display negative rhombohedral crystal shape whereas in datolite, inclusions tend to be more ovoid, prismatic or irregular. Microthermometric determinations were carried out on a SGE heating stage which had been calibrated with chemicals of accurately known melting point (methyl benzoate, distilled H_2O, benzoic acid, $NaNO_3$, $K_2Cr_2O_7$, $PbCl_2$).

Heating runs on fluid inclusions in calcite yielded a range in homogenization temperature (T_h) of 140°217°C, with a mean T_h of 183°C; inclusions in datolite have a T_h range of 145°209°C (mean T_h =171°C) (Fig. 4). The difference in mean T_h between datolite- and calcite-hosted inclusions is not considered significant due to the small number of measurements obtained on datolite. All inclusions homogenized to the liquid phase and repeat determinations yielded a precision of ± 5°C.

Freezing runs to determine the melting temperature of ice (T_m) were difficult due to small size of inclusions and the double refraction of calcite. However, several inclusions in datolite yielded a value of T_m of -1.4 ± 0.5°C. Using the equations of Potter *et al.* (1978), this value converts to 2.3 ± 0.8 equivalent weight (ewt) % NaCl. The calculated fluid salinity is probably a maximum value as it assumes no contribution to freezing point depression by dissolved CO_2 which has been shown to give erroneously high calculated equivalent NaCl values (Hedenquist and Henley, 1985). As vein calcite accompanies the borosilicates, it is implicit that CO_2 was at least a minor fluid component and thus NaCl values are likely to be <2.3 ewt %.

There is no evidence for boiling or effervescence in fluid inclusions in the borosilicate-bearing veins (i.e. trapping of coexisting liquid- and vapour-rich inclusions). Thus the pressure on the fluid at the time of entrapment was greater than the vapour pressure and hence a pressure correction must be applied. From the boiling curves of Haas (1971), it is estimated that at least 100 m of cover (at hydrostatic pressure) would be needed to prevent fluids of 2.3 ewt % NaCl from boiling at 180°C (the approximate average of all vein fluid inclusion T_h values; Fig. 4). This estimate is clearly a minimum as current topographic relief between Devils Elbow and the Tertiary basalt-capped plateau to the east (Fig. 1) is 200-250 m. A more realistic depth of formation for the veins would be approximately 2-4 km, based on analogies with quartz veins hosting Au-Sb-W-As mineralization in the Nundle area and the southern part of the New England Orogen generally (e.g. Comsti and Taylor, 1984; Nano, 1987; Ashley and Hartshorn, 1988) and the fact that the vein-controlling structures are brittle phenomena. On this assumption, lithostatic pressures would be in the range 0.6-1.2 kb and would require a pressure correction of +50-100°C, utilizing the curves of Potter (1977). This would imply that the borosilicate-bearing veins formed at an average temperature of between 230° and 280°C.

The estimated conditions for vein formation and the nature of the vein fluids are

somewhat similar to those deduced for the vein Au-Sb-W-As occurrences in the Nundle district. T_h data from over 370 fluid inclusions in these veins have an uncorrected range of 139°-365°C, with a bimodal distribution of T_h at 190°C and 250°C. Ashley and Hartshorn (1988) also showed that the fluids were CO_2-bearing and averaged 4 ewt % NaCl. Applying the above pressure correction to the Au vein data, the bimodal peaks fall at approximately 260°C and 320°C. It would therefore appear that the borosilicate veins formed under conditions analogous to the lower part of the T_h spectrum for the Au veins.

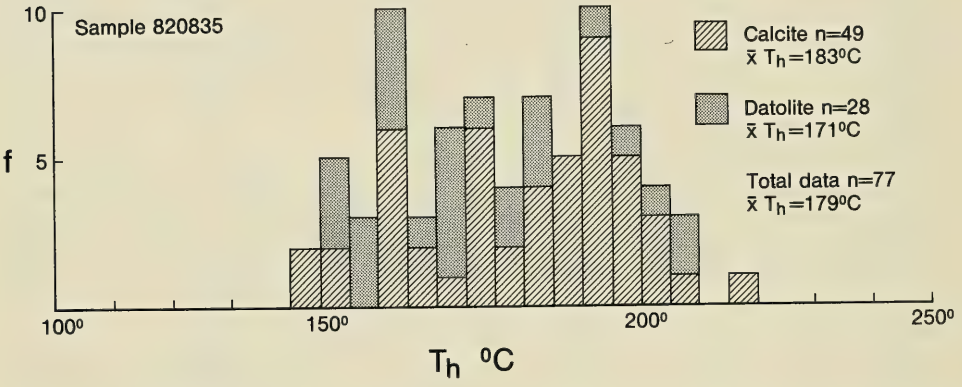

Fig. 4. Fluid inclusion homogenization temperatures (T_h) from vein calcite and datolite, sample R63080, Devils Elbow.

Discussion

Metamorphism and Timing of Vein Formation. Rocks hosting the borosilicate-bearing veins at Devils Elbow have the following (non-vein) critical metamorphic parageneses:

1) Limestone: grossular + diopside + vesuvianite + calcite + clinozoisite;
2) Siltstone: actinolite + diopside; and
3) Dolerite: actinolite + chlorite + epidote + titanite ± pumpellyite.

If it is assumed that pressure operative in the metamorphism (which was static in character) was relatively low, e.g., approximating 2 kb, then the assemblages indicate temperatures of at least 400°-425°C with a low mole fraction (X) of CO_2 (X_{CO2} probably <0.02). These parameters are suggested by the presence of vesuvianite (in the absence of quartz) (e.g., Hochella *et al.*, 1982), presence of grossular and absence of prehnite (in non-vein assemblages) (e.g., Liou, 1971; Winkler, 1979; Liou *et al.*, 1985). Although diopside may form below 350°C, its occurrence further confirms low values of X_{CO2} (e.g. Labotka *et al.*, 1988). Since the mafic rocks contain typical actinolite + chlorite + titanite assemblages, maximum temperatures at 2 kb (and at oxygen fugacities below the hematite-magnetite buffer) are not likely to have exceeded 450°-475°C, according to the experimental work of Moody *et al.* (1983). The occurrence of pumpellyite in the dolerite raises problems as Schiffman and Liou (1980) have shown that at low pressures (2-3 kb), MgAl pumpellyite is stable only to temperatures of 330°-350°C. It is possible that the mineral is metastable, having been insulated from prograde breakdown reactions by its typical occurrence in albitized plagioclase cores.

Mafic and volcaniclastic rocks in the Gamilaroi terrane elsewhere in the Nundle district characteristically contain albite + chlorite + titanite ± prehnite ± pumpellyite ± actinolite ± epidote ± carbonate ± relict clinopyroxene ± magnetite (e.g. Benson, 1915; Vallance, 1960; Chappell, 1968; Cross, 1974; Morris, 1988; Ashley and Hartshorn, 1988). Such assemblages probably straddle the prehnite-actinolite and prehnite-pumpellyite facies, which at pressures of <3 kb are restricted to temperatures below 350°C (e.g. Liou *et al.*, 1985). The presence of apparently higher-grade rocks at Devils Elbow are interpreted as the result of later thermal metamorphism by the Permian Duncans Creek Trondhjemite which crops out 6 km to the northeast (Fig. 1) but probably underlies a considerable region to the west and south of the intrusion. This concept is consistent with the occurrence of contact metamorphosed dolerite and sediments elsewhere east of Nundle (Morris, 1988) and with the fact that much of the serpentinite along the Peel Fault in the area is antigoritic (Ashley and Hartshorn, 1988).

The borosilicate-bearing veins cut the metamorphic assemblages and thus if the latter are related to the intrusion of the Duncans Creek Trondhjemite, then the former must be no older than middle to late Permian (e.g. Cross, 1983; Hensel *et al.*, 1985). Timing of the borosilicate veins could therefore be the same as that deduced by Ashley and Hartshorn (1988) for the formation of the vein Au-Sb-W-As mineralization in the Nundle goldfield, that is, probably no older than late Permian. It is also possible that the borosilicate veins are simply another manifestation of the Nundle goldfield veining, examples of which occur within 300 m of Devils Elbow. Borosilicate veining may be temporally related to the same vein-forming thermal event and to similar brittle-style structural control. It is probably no coincidence that the borosilicate-veined samples are anomalous in As (Table 2) and that rare tourmaline occurs in alteration selvedges about Au-bearing veins in the Nundle goldfield (Ashley and Hartshorn, 1988).

Conditions of Vein Formation and Component Sources. Field and petrographic evidence dictate that the borosilicate-bearing veins post-date the host rock metamorphic assemblage which may have developed at 400–450°C and pressures <3 kb. From fluid inclusion and mineralogical data, the veins formed at 230–280°C and possibly at pressures of 0.6-1.2 kb. Hydrothermal fluids were dilute (<2.3 ewt % NaCl), possibly CO_2-bearing and transported SiO_2, B and As in solution. The source of these components is speculative with possible alternatives including the enclosing marine sedimentary and basaltic package, granitic intrusives or from deeper crustal metamorphic devolatilization reactions. An intrusive-related magmatic source is considered unlikely for B as the nearby Nundle Suite intrusives (e.g. Duncans Creek Tronhjemite) are not known to contain late- or post-magmatic tourmaline and have primitive I-type (metaluminous) characteristics (e.g. Hensel *et al.*, 1985). These properties are quite unlike tourmaline-bearing granites which are typically felsic peraluminous in nature (e.g. Pollard *et al.*, 1987). A source of B from marine sediments (e.g. shales average 120 p.p.m. B; Harder, 1974) or from B previously fixed in basaltic rocks by interaction with seawater (e.g. Spivack and Edmond, 1987) is considered more plausible for the Devils Elbow borosilicates and for axinite occurrences elsewhere in the Nundle district. Remobilization of B from this source may have attended the shallow crustal hydrothermal fluid circulation accompanying the formation of the Nundle goldfield Au-Sb-W-As veins. Confirmation of these speculations may have to rely on future stable isotope determinations, including $\partial^{11}B$ values for the vein borosilicate minerals.

Summary and Conclusions

The calcium borosilicate mineral axinite has been known for many years in mafic

rocks of the Devonian Tamworth Group in the Nundle district (e.g. Benson, 1913). However, new exposures at Devils Elbow, 4 km east-southeast of Nundle, have revealed simple and anastomosing veins containing axinite and the comparatively rare borosilicate, datolite. The veins, up to 3 cm wide, occupy brittle structures in steeply dipping recrystallized bioclastic limestone (informally termed Devils Elbow Limestone Member), massive dolerite and basalt, and bedded cherty calcareous siltstone grading into volcaniclastic sandstone. Datolite-bearing veins, containing associated calcite, quartz, chlorite and prehnite, are restricted to the limestone and cherty calcareous siltstone whereas axinite-bearing veins, with associated quartz, calcite and chlorite, occur within the mafic rocks and volcaniclastic sandstone. It is probable that host rock composition has influenced the speciation of the borosilicates, i.e. datolite being found in rocks with low Fe, Mn and Al contents and axinite in rocks with significantly greater concentrations of these elements.

Datolite is pale brown, pale green or white and analyses indicate it is close to stoichiometric $CaBSiO_4(OH)$. Axinite forms pale mauve prisms compositionally falling into the ferroaxinite field of Sanero and Gottardi (1968). There is a considerable range of Mg, Fe and Mn contents with Mg being negatively correlated with Fe and Mn. Whole rock chemical analyses of veined and unveined samples of limestone and dolerite indicate that SiO_2, B and minor As were introduced during the vein-forming event. Background B concentrations in the host limestone and dolerite are considerably enriched above values for average limestone and MORB-type basaltic rocks (*cf.* Harder, 1974; Spivack and Edmond, 1987) and could imply prior introduction from a seawater source.

Vein minerals contain simple 2-phase fluid inclusions, although only those in calcite and datolite were large enough to obtain microthermometric data. Homogenization temperatures range from 140°-217°C with a mean of 179°C and although only a few inclusions were suitable for freezing point determination, an ice melting temperature of -1.4° ± 0.5°C was obtained, indicating a maximum fluid salinity of 2.3 ewt % NaCl. CO_2 is likely to have been at least a minor component of the fluid which was not boiling or effervescing. Based on an assumed depth of formation of 2-4 km for the borosilicate veins (similar to deduced formation depths of Au-Sb-W-As-bearing veins in the Nundle district and elsewhere in the southern part of the New England Orogen), a pressure correction of +50°-100°C on the T_h values is required, yielding average vein formation temperatures in the range 230°-280°C.

Estimated vein formation conditions are at lower temperatures than those enjoyed by the enclosing rocks which show anomalously high metamorphic grade in comparison to Tamworth Group rocks elsewhere in the Nundle district. Metamorphic temperatures in the Devils Elbow-Hanging Rock area may have attained 400°-450°C and are attributed to contact effects of the nearby (?underlying) Permian Duncans Creek Trondhjemite. As borosilicate-bearing veins cut the metamorphic assemblages, the vein formation may be no older than late Permian and therefore probably coeval with the Nundle goldfield vein Au-Sb-W-As mineralization.

It is concluded that borosilicate-bearing veins at Devils Elbow, and elsewhere in the Nundle district, are another manifestation of the extensive Au-bearing vein systems. Borosilicate veins formed at slightly lower temperature and from more dilute hydrothermal fluids, but are otherwise not dissimilar (*cf.* Ashley and Hartshorn, 1988). Tourmaline occurs locally in association with the former, and As is anomalous in the latter; these chemical phenomena are viewed as common links. The source of B for the veins is unlikely to have been from granitic intrusives in the region, but could have been remobilized from marine sediments and mafic rocks which had undergone prior B fixation from seawater. The vein-forming event in the Nundle district, including both

the Au-Sb-W-As- and borosilicate-bearing veins, could be temporally related to the intrusion of the nearby Nundle Suite granitoids (e.g. Duncans Creek Trondhjemite and Mt Ephraim Granodiorite), but evidence from the mineralized veins suggests that the veining and hydrothermal activity is later (Ashley and Hartshorn, 1988). An alternative view is that the event is linked temporally to the intrusion of the late Permian Moonbi Suite plutons in the southern New England Orogen, not necessarily to the intrusives directly, but to the causative deep crustal thermal regime.

Acknowledgements

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Jupiter Botanicus in the Bush: Robert Brown's Australian Field-work, 1801-5

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[Delivered 22 March 1989]*

Synopsis

Australia's 'Celebration of a Nation' in 1988, in my view, turned out to be an apotheosis of the second-rate as far as recognition of talent in the sciences of natural history was concerned. The values paraded were not those of The Linnean Society of New South Wales. It seems we treasure heroes publicly overlooked. But our heroes ought not be thus forgotten, and the conjunction of anglophone Australia's bicentenary with that of The Linnean Society of London encourages me to consider one of relevance to both. Australian students of systematic Botany are familiar with the name Robert Brown, that of a figure linked inextricably with the history of the London society and, albeit less directly, with that of our own. They know Brown came to Australia as naturalist with Matthew Flinders on H.M.S. *Investigator*. Yet few seem to be aware of what Brown did here, where he went during the period 1801-5 to collect the material on which so many of the plant taxa they know were based, or that he also examined animals, rocks and minerals as well as plants. The failure of Australian scientists and historians to be seriously inquisitive about the activities of a pioneer who contributed mightily to scientific knowledge is both remarkable and a reproach. A main purpose of this address is to provide a calendar of Brown's field-work in Australia. It is hoped thereby readers will gain some better understanding of what lay behind the 'R.Br.' attached to hundreds of Australian plant names.

ORIENTATION

At our society's Annual General Meeting in 1889 my presidential predecessor, W. J. Stephens [1829-1890], dismissed unceremoniously his fellow colonists' efforts to mark completion of the first hundred years of European settlement in Australia: 'rather more than a year ago, many persons were endeavouring to get the Centenary celebrated with universal rejoicings. The most absurd proposals were heard exploding in all directions, in the vain effort to stimulate an enthusiasm which had no substance or basis. Each agitator called upon everybody else to be enthusiastic, but no symptoms of enthusiasm were visible, excepting those which were well paid for out of the public purse' (Stephens, 1889: 1781). Stephens continued, more despairing than enthused: 'no one can deny that we have kept our Centennial year in a way not lightly to be forgotten. With political squabbling and scuffling inside and outside Parliament, with strikes . . ., with clamour against Chinese labour . . ., and with a disastrous drought . . ., we must admit that we have something to remember'. Only the inauguration during 1888 of the Australasian Association for the Advancement of Science (later, ANZAAS) appeared a worthwhile enterprise to Stephens. He welcomed it by the way before going on to devote the main part of his address to society business and a review of recent advances in science. His successor at the time of the sesquicentenary, E. C. Andrews [1870-1948], also a geologist, did not even bother to nod to the national festivities of 1938 in his presidential address.

Some beyond our society may be surprised to learn how unenthusiastically in their

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time and office Stephens and Andrews reacted to the celebration of what by general consent were notable anniversaries. Neither man could fairly be accused of want of patriotism and the concerns of The Linnean Society of New South Wales, then and still the only voluntary body anywhere in the country committed specifically to promoting knowledge of mineral, plant and animal Nature, are without doubt related to the history of anglophone Australia. Why then did these presidents decline to join the rejoicings? For me, having experienced the way the bicentenary went last year, the answer is not hard to find. The values espoused by our society and those represented as prized by the Australian community at large still run no risk of collision. It might have been otherwise. The land to which the first, mainly unwilling and unsophisticated colonists came in 1788 was practically unknown to Europeans. Nature lay awaiting exploration and study but the distant promoters of settlement had perceived no need to send with the First Fleet or its successors any naturalist who could have served as expert guide. The early settlers had to make with Nature what accommodation they could. Exploitation rather than appreciation of the natural environment was forced upon our ancestors. It has since, alas, become practically habit. Australian history as commonly propagated is a stage largely for officials and exploitative entrepreneurs of one sort or another. Those who by quiet dedication established our knowledge of Australian Nature rarely get noticed. Davison's study (Davison *et al.*, 1987: 1-29) of the centennial celebrations shows that self-made men foisted upon their community in 1888, what irked Stephens. Material prosperity, actual or hoped-for, mattered more to the then rulers than anything intellectual. By delicious chance, however, that year 1888 yielded also the second and final series of *Essays in Criticism* (1865, 1888), the work in which the English poet and educator Matthew Arnold [1822-1888] drew convincing attention to the prevailing philistinism of his countrymen. Transportation to what once were known as English colonies had brought more than people; distance did, and does, not insulate Australians from Arnold's strictures. One hundred years on, little seems to have changed here. True, the bicentenary was celebrated on a grander scale, with matching expense, than previous anniversaries but the perceptions which mattered in 1888 are still to the fore. Stephens and Andrews opted to stand aside from the clamour in their times. While ready to identify with them, I do not intend to follow. Our society's values deserve an airing.

The very name of our society in a way is its affirmation. According to Walkom (1925: 10), members at the first meeting (29 October 1874) came up with but two suggestions regarding an appropriate name. One at least thought we should be 'Banksian' but 'Linnean', promoted by W. J. Stephens, easily prevailed. Although A. B. Walkom [1889-1976] inclined to the view Stephens meant to commemorate links with The Linnean Society of London long enjoyed by members of the Macleay family (W. J., later Sir William, Macleay [1820-1891] had accepted our society's inaugural presidency), the decision of 1874 indirectly or directly pays tribute to the Swedish scientist Carl von Linné, earlier Linnaeus [1707-1778]. Our founders adopted as exemplar one whose life practically was given over to careful study of all branches of Nature and instruction of others in knowledge of its order and variety, by lectures to his pupils or 'apostles' (Jonsell, 1982) and by his voluminous writings. The choice, of course, implied no desire to resurrect the science of Linnaeus's day. Rather, it proclaimed the hope that members would seek to emulate the ways of an outstandingly active and fruitful investigator of Nature for the sake of knowledge. A matching exhortation to activity comes with the appropriately classical (Linnaeus lectured and wrote in Latin) motto used by the society since its early days: *integros accedere fontes*, to approach untainted springs. Members know the motto from the covers of the *Proceedings* but to judge from questions asked few are aware of its origin. The three words, one emended in a way which seems to me to implicate

W. J. Stephens, teacher of Latin as well as Natural History, are from a sentence found twice in the didactic poem *De Rerum Natura* (Bk I, 927; Bk IV, 2) of the 1st century B.C. philosopher-poet Titus Lucretius Carus, generally known as Lucretius: *juvat integros accedere fontis atque haurire*, 'What joy it is to light upon virgin springs and drink their waters' (as translated by R. E. Latham in the Penguin Classics edition, 1951). The poet's joy is his reward as 'sweet love of the Muses', custodians of knowledge, grants him 'strength to pioneer through pathless tracts of their Pierian realm where no foot has ever trod before' (Latham translation). Lucretius may never have practised what he preached and been a naturalist in any conventional sense but his aim that readers of the poem will 'gain insight into the nature of the universe and the pattern of its architecture' (Latham) serves to link our motto and eponym.

'The cultivation and study of the science of Natural History in all its branches' has ever been the guiding principle of our society. It fitted Linnaeus's consuming purpose in life, but what of Sir Joseph Banks [1743-1820]? The decision of 1874 showed clearly enough most of our founders thought Banks no competitor to Linnaeus. A group committed to 'Natural History in all its branches' had reason to question the suitability as model of one whose interest in the field hardly extended beyond a partiality to Botany. Banks, for instance, had been content to leave what Linnaeus termed the mineral kingdom as no more than a source of income (Vallance, 1986: 151). As to 'cultivation and study' our founders could respect Banks as a supportive patron of selected scientific enterprises but where, they might have asked, was the evidence of his engagement in the actual work of science? He had, indeed, when young been active as a collector, chiefly of plants, but Banks's published works, those issued in his lifetime, dealt rather with antiquities, agriculture and the economy of estates than with Botany. Linnaeus matched our founders' resolve to promote active participation and breadth in scientific effort; Banks did not. Yet, without question, that resolve set The Linnean Society of New South Wales apart in a community which already accepted Joseph Banks as a notable figure in its history and accorded him credit as a sort of founding genius of Nature study here. And as recent bicentennial events have shown, Banks remains a congenial hero to many Australians. Banks continues to divide. Any examination of our society's historical position must admit as much and seek to show why.

The one identified supporter of the society going 'Banksian' in 1874 was a retired naval officer, Thomas Stackhouse [*c*1832-1886], honorary secretary 1874-9 and reputedly a keen collector of plants. What little I know of him suggests Stackhouse was a public-spirited man with some range of interests in science not put to use as a practitioner. If he made any particular scientific study the results are lost. There is not even a record of his contributing an exhibit at a monthly meeting. What attracted Stackhouse to Banks? Perhaps it was Banks's early interest in plant-collecting, his naval connection through the voyage on H.M.S. *Endeavour* (1768-71), or his devoted service to The Royal Society of London. The reason is unknown but Stackhouse would have been neither the first nor the last to fix an enthusiasm for Banks on some perceived alliance of interests incidental to science. Birth, wealth and connections smoothed Banks's way in life; connections, real or supposed, continue to serve. Assumption of privilege secured places for him and his party as supernumeraries on *Endeavour* and the lion's share of praise for its success when the expedition returned home (Beaglehole, 1974: 273-4). He was fortunate too to have as colleague on that voyage one of Linnaeus's 'apostles', D. C. Solander [1736-1782], a man with some of his mentor's versatility but far less, it must be admitted, of Linnaeus's capacity for sustained effort. On *Endeavour* at least Solander did supply more than intellectual ballast. He and Banks, and Banks's assistants, kept impressively busy on lines consistent with the patron's interest, that is chiefly with plants and animals. Geological matters, and one of Solander's few published works dealt with Tertiary fossils

(Brander, 1766), were more or less ignored. After the voyage Solander went back to his post at the British Museum but took on extra part-time duty with Banks as his librarian and curator. It was then Banks's intention to prepare a Botany of the voyage, supposedly a 'common effort' (Rauschenberg, 1968: 42) with Solander though the extent to which Banks gave science to what remains unpublished is far from clear. Rauschenberg (1968: 42) admits some of the blame for the work lapsing may have been due to Solander's failure to resist the allures of London society but argues rather that 'Banks never pushed the project' — an odd claim if Banks, in fact, had been an actively contributing author as well as underwriter. Yet it is Banks who emerges shining to posterity, as even the title of the *Banks' Florilegium* (Adams, 1986), issued 1980-8, shows. The man who commissioned the original plates for the Botany of the *Endeavour* voyage gets all the credit, it seems.

Banks's dependence on Solander is not easily exaggerated. Solander brought Linnaean expertise to the association and after Banks assumed the presidency of the Royal Society with its attendant duties in 1778 responsibility for *Endeavour* Botany must have fallen even more heavily on the part-time curator and Banks's artists. Was it a coincidence that systematic work on the plants effectively came to a standstill after Solander's sudden death? Nor did the loss of Solander impinge only on *Endeavour* Botany. In July 1783 one who had been on the voyage, J. M. Matra (alias Magra) [1746-1808], wrote to Banks enquiring about a reputed scheme to make settlements in the South Seas. The following month Matra claimed Banks's approval of 'A Proposal for establishing a Settlement in New South Wales' (King, 1985: 12-20) then being lodged with the British government. An official Committee of Enquiry into Transportation was set up in consequence and on 10 May 1785 Sir Joseph Banks gave evidence (King, 1985: 58-62) before it in favour of a colony at Botany Bay. By then Banks had had at least two years to refresh his memory of the place visited on the *Endeavour* voyage in 1770. Yet the answers he offered to questions about the character of Botany Bay appear remarkably uninformed. Reading the transcript one is led to wonder if Banks had not left to Solander the serious business of observing Nature there. In 1785, however, there was no Solander and the word of the Royal Society's president had to be authoritative. Botany Bay became the appointed place for settlement. That it, in fact, was quite unsuitable only became apparent in January 1788 when Captain Arthur Phillip [1738-1814] reached there with the First Fleet. The most cursory inspection convinced Phillip he would have look elsewhere. He was in process of moving people and stores from Botany Bay to Sydney Cove when the expedition led by J. F. de Galaup, Comte de la Pérouse [1741-1788] arrived in the bay for respite. Phillip soon discovered the French vessels carried scientific staff and took what advantage he could of the brief presence of a naturalist. Governor Phillip had cause not only to rue Banks's inept advice regarding Botany Bay but also his failure to urge the appointment of any scientific adviser to the colonizing venture. Those who regard Banks as the 'Father of Australia' would do well to contemplate the baronet's less-than-glorious role at the outset.

Sir Joseph Banks, it seems, has never lacked admirers ready to put the worthiest gloss on their hero's life and works. Those of the present must have found last year's bicentennial celebrations endlessly satisfying. They, and we, heard or read in 1988 of Banks the accomplished traveller, great scientist and patron of science, a model of eighteenth-century Enlightenment (*pace* Buffon *et al.*) and, of course, Father of Australia. No one but Banks had much credit for the study of Australian Nature. The claims themselves were nothing new. What distinguished these from past celebrations was the extent to which many scientific bodies in this country now showed a readiness to identify with Banks. Not only were portrait busts of Banks set up in the botanical gardens of Canberra and Sydney but the Australian Academy of Science, in concert with the state Royal societies, sponsored Banks Lectures in various centres. The busts in their

situations might commemorate Banks's long and practical association with the Royal gardens at Kew but what of the lectures, public nods from science, being dedicated only to Sir Joseph Banks? One wonders how carefully the promoters of those lectures had examined the evidence before deciding to ride the Banksian bandwagon.

The sponsors of Banks Lectures must have forgotten, if they ever knew, what an undeniably distinguished scientist and contemporary, Sir Humphry Davy [1778-1829], himself president of The Royal Society of London 1820-7 — a place, by the way, Banks thought him 'rather too lively to fill ' (Treneer, 1963: 186), wrote of their hero: 'He was a good-humoured and liberal man, free and various in conversational power, a tolerable botanist, and generally acquainted with Natural History. He had not much reading and no profound information. He was always ready to promote the objects of men of science, but he required to be regarded as a patron, and readily swallowed gross flattery' (J. Davy, 1836: II, 126). Even early this century Smith (1911: 300-1) could allow Davy had there commented 'not ill-naturedly' but since then Banksian devotees have tended to close ranks, sniffing at the bad manners of the humbly-born Davy, envious of an established gentleman. Thus Cameron (1952: 158) disposes of the sketch by claiming Davy 'never liked him [Banks]'. O'Brian (1987: 298-9) goes further: 'even quite strong resentment cannot without an even stronger additive of ill-nature, account for Sir Humphry Davy's often-quoted remark'. Carter (1988: 440) simply dismisses the sketch as 'that bleak and pejorative comment'. This modern school of Banksians allows its hero all the privilege he himself appropriated in life (Beaglehole *in* Banks, 1962: I, 23) and either damns as a detractor or ignores any who questions. The work of an experienced Australian botanist learned in the history of his subject, McGillivray (1971), for instance, which agrees with Davy on Banks's botanical expertise rates no mention in Carter's extensive bibliography (Carter, 1987). But then a conclusion like 'The outstanding and the incompetent may be remembered for their botany through two hundred years, but not the "tolerable" ' (McGillivray, 1971: 15) is hardly ambrosia to a hagiographer. Fortunately, there are also other judicious sources, chief among them Beaglehole (*in* Banks, 1962) and Beaglehole (1974). Those studies, along with his meticulous editions of Cook's voyages, in my view show why the historian J. C. Beaglehole [1901-1971] so outshone all others of his profession in Australasia. Beaglehole (*in* Banks, 1962: I, 123-4) cites Davy on Banks but parts company with the special-pleaders after admitting the contrasted origins: 'Davy came from a quite different stratum of society, Davy was all concentration, a laboratory man, Davy belonged to — was the maker of — a new age'. Beaglehole then goes on to complete the picture: 'Banks, we may conclude, had not the instinct of thoroughness'. Banks was not a scientist in the sense Davy was; nor was he one like Linnaeus.

It is possible, however, our colleagues joined the Banksians in 1988 not from some mistaken thought that Banks was a scientist but rather from a desire to be identified with his perception of science. Again, I turn to Humphry Davy. Following the custom whereby fellows submitted notice of their discoveries to the president of the Royal Society, Davy in 1815 sent Sir Joseph details of his miners' safety-lamp. This time he received an acknowledgment: 'Much as by the more brilliant discoveries you have made, the reputation of the Royal Society has been exalted in the scientific world, I am of opinion that the solid and effective reputation of that body will be more advanced among our contemporaries of all ranks by your discovery, than it has been by all the rest' (Banks to Davy, 30 October 1815; letter in the Royal Institution library, London). The isolation of potassium and sodium in 1807 or proof of the elementary nature of chlorine (1810) had elicited no such presidential praise. The safety-lamp was different; it was useful. A mine-owner himself even if his properties were not plagued with fire-damp, Banks knew the commercial advantage offered by Davy's invention would be widely

welcomed. This was Banks the 'improver' in action. He could appreciate science where it served a useful purpose. It gained public esteem for science and such esteem was what Banks particularly prized. He had long been active as a patron of efforts to improve agriculture and horticulture. Botanical collectors knew of his special interest in plants which might be turned to advantage by cultivation. That interest, by the way, is now being appropriately acknowledged in the Sir Joseph Banks Centre for Economic Botany under development at Kew.

Davy's perception of science could hardly have been more divergent. Davy certainly relished his share of public esteem and showed no reluctance to engage in 'useful' projects but whereas Banks could regard such work as a sufficient purpose Davy made sure it did not interfere with what he took to be the overriding aim of science, enlargement of knowledge of the natural world. His response as 'The Unknown' (H. Davy, 1831: 240-6) to the assertion 'It does not add much to the dignity of a pursuit, that those persons who have followed it for profit have really been most useful' sets a perspective Banks would have thought eccentric. Throughout his sadly short career Davy remained convinced the worth of any scientific discovery — and his own researches ranged across biological and geological as well as purely physical science — is independent of considerations of practical utility (J. Davy, 1858: 58). It may not be spoken of at South Kensington where Banks resides in marmoreal splendour but it was Davy, not Banks, who opened the way for a national facility to foster research in Natural History (Hartley, 1966: 129). Davy's scheme for a separate department of the British Museum 'with a separate government' may have foundered in the corridors of Whitehall but it foreshadowed what came into being some sixty years later. Yet one will look in vain for acknowledgment of Davy in the semi-official history of the British Museum (Natural History) by Stearn (1981) where Banks a material but hardly intellectual benefactor, patron rather than practitioner of science, appears in abundance.

The values fostered by Davy, as earlier by Linnaeus, that science principally should be about increasing knowledge have been shared by most significant discoverers in science. That 'new age' Beaglehole credited Davy with making also marked a return to a liberal perception of science curtailed for so long by the selective, utilitarian style imposed by Banks both privately and as president of the Royal Society. It was not that Davy disavowed patronage, or refused to find merit in any of Banks's promotions. Banks, indeed, had an acknowledged knack for employing people who performed beyond expectations. And Davy knew his own career owed much to the support of The Royal Institution of Great Britain, a body set up with decidedly practical aims but which had shown itself open to promoting science in general. Patronage, as Davy was aware, had to be sympathetic and open-minded, not narrowly-conceived, if it were to allow talent full opportunity for enlarging scientific knowledge. That message is worth remembering now as a philistinism of 'relevance', of 'applicability', propagated widely within governments and business, in educational and even some scientific circles, threatens to draft ever more scientific effort in directions congenial to holders of influence. One wonders, indeed, if the enthusiasm for Banks certain Australian scientists discovered last year was at least in part a gesture of 'gross flattery' towards latter-day patrons as intrusive and mostly as utilitarian as Banks was in his time. Whatever the reason for the fervour, the challenge to The Linnean Society of New South Wales to keep asserting its intellectual purpose, to keep helping 'to approach untainted springs' remains.

There was, of course, little enough reason here in 1988 to remember Davy the man, or Linnaeus for that matter. Apart from a few items of Australian business referred to the Royal Society under his presidency, Davy enjoyed no particular link with this country though it and its inhabitants oocasionally came into his thought (e.g. H. Davy, 1831:

74, 147-8, 229). Thought, however, was hardly a significant element in the public affairs of 1988. Sir Joseph Banks held every advantage. His links, the visit on *Endeavour* in 1770 and the continuing interest in colonization of the country, were known to Australians from schooldays. No sophisticated pleading is required to secure a place for him in any general celebration of our past. But to those charged with generating public enthusiasm Banks the 'improver', the promoter of exploitative activities, had other attraction; they could understand and identify with his aims. Banks the utilitarian patron, the man of 'no profound learning' according to Davy, qualified nicely for prominence in the official bicentennial celebrations, managed as they were by government-sponsored committees on which business and administrative interests held greater influence than those of the mind. Public events thus came to be marketed, marketed as entertainments rather than as opportunities for reflection and learning. The circumstances determined that where science emerged in the programme it was 'useful' science, with use embracing diversion, not science as knowledge. As an example I take the touring exhibition of treasures from British collections, chiefly those of the British Museum (Natural History). The Introductory Message in the book (Steven, 1988: 5) of the exhibition set an unmistakable tone: '. . . a stunning exhibition . . . this entertaining and delightfully presented volume . . . We wish *First Impressions* well in the South Land, and its audiences great enjoyment'. South Land indeed; was it expected Australians could only gape? It seemed so. The exhibition brought fascinating images of Nature as historical documents with barely a hint as to where those first impressions led in terms of understanding. Indeed the assertion that in 1815 'British curiosity about Australia surrendered its scientific emphasis to a commercial concern' (Steven, 1988: 89) appeared to dispose of the matter. But why 1815, and why to other aspects left unconsidered? It appeared those who mounted *First Impressions* were expert in display, in public relations or whatever now puts science and learning at risk as museums seek to become 'accessible' as places for entertainment. *First Impressions* made a dazzling show but where was the scholarly substance? No doubt the promoters felt confident a 'solid and effective reputation', a Banksian reputation, could be achieved most readily by avoiding tiresome detail.

Ever since one of my great-great-great-grandfathers, and others, began teaching the youth of this country, in the 1790s in Sydney, there have been anglophone Australians capable of some sophistication. Yet it has been a talent little used for much beyond 'getting and spending', as Wordsworth put it. Ours may be a lucky country, the pithy term of one modern commentator, but its population has yet to establish any widespread respect for critical intelligence. The fare dished up last year by way of celebrating the bicentenary seemed to acknowledge this. Perhaps it was appropriate though I had hoped for better and there recent experience encourages me. It was my privilege early in 1988 to address geological colleagues gathered in Brisbane to celebrate 'Achievements in Australian Geoscience' over two centuries. There have been, of course, many achievements in that and other sciences worthy of remembrance but the occasion also gave me the opportunity to raise questions about originality, about quality in the science, and to caution against complacent acceptance of fashions (Vallance, 1988). Serious discussion ensued for days afterwards. Members of a profession more involved with material progress through exploitation of the environment than most others in the natural sciences showed themselves impressively ready to pause and reflect on what they owe to those who have been prepared to challenge the assumptions of authority. I look forward to the day Australians will recognize that the adulation of Joseph Banks during their bicentenary was largely a result of assumptions.

It comes as no surprise that one rated no better than 'a tolerable botanist' (McGillivray, 1971) has no place, even among the least distinguished, in a classification of naturalists compiled about 1847 by Edward Forbes [1815-1854], later Regius Professor

of Natural History at Edinburgh (Wilson and Geikie, 1861: 414-7). Yet among those of Forbes's highest class, that to which 'the greatest leading minds belong' — a group of four including Aristotle and Linnaeus, is the name of the first outstandingly-able man of science to work in this country, a man whose career effectively began in Australia. Here surely was an appropriate candidate for glory in the bicentennial celebrations but it did not turn out that way. The public scientists preferred Banks lectures and although *First Impressions* allowed a nod to this man so respected by Edward Forbes, Steven (1988: 73) has his portrait (with artist's name misspelled) reproduced smaller than any one of the three portraits of Banks, four counting a caricature, present in the book of the exhibition. Robert Brown [1773-1858], alas, is all but unknown to most Australians; nor should the present tense only be used. A well-informed newcomer to Melbourne felt moved by experience there in the 1860s to annotate as follows the passage concerning Brown in what is now my copy of Wilson and Geikie (1861: 416): 'This common name of Robert Brown is one I dare be sworn has scarcely been heard of by even a very few of Australian Colonists, yet is it one intimately connected with Australia — Humboldt entitled him 'the first of European Botanists' — He accompanied Flinders as naturalist, the then young Franklin being a shipmate, as midshipman. Sir Joseph Banks and Dr. Solander had previously gained a slight knowledge of the Australian Flora, but Dr. Robert Brown was the first to make an extensive acquaintance with Austrn. Botany, and to this day & ever will be considered as a leading authority in it'. The remark on Franklin (Sir John Franklin [1786-1847]), I believe, serves to identify the writer who signed his name Robert Goodsir in the book. Lonsdale (*in* Goodsir, 1868: I, 9-10) records that Robert Goodsir, a medical graduate and brother of the Edinburgh anatomist John Goodsir [1814-1867], close friend of Edward Forbes, had sailed twice to the Arctic on expeditions sponsored by Lady Franklin to seek evidence of her husband's fate and of those who sailed with him in 1845. Among the lost was another Goodsir brother, Harry, who had gone with Franklin as surgeon and naturalist. Robert Goodsir's intimate connections with active students of the sciences of Natural History lend weight to his observations on Brown, as well as on Banks and Solander. I have no idea what became of him in Australia but suspect his stay was not long; his book had a new owner by 1870.

Goodsir's reference to Alexander von Humboldt [1769-1859] and his enthusiasm for Robert Brown was notably apt. The same Humboldt even rated him *Botanicorum facile Princeps*. Although Brown had the respect of a select few of his countrymen, it was in continental Europe, especially in Germany, that the innovative and intellectual quality of his work gained most profound admiration. By 1855 his distinguished colleague Karl von Martius [1794-1868] of Munich was addressing Brown as *Jupiter botanicus*, the title adopted by Mabberley (1985) for what, remarkably, is the first detailed biographical study of the most 'philosophical' botanist of his period — ' "philosophical" because he combined the descriptive and the experimental: on the one hand . . . the patient descriptive approach . . . the bibliographical expertise . . . as well as the acute powers of observation and interpretation necessary to a herbarium taxonomist; and, on the other, the flair and zeal for experiment with new approaches — principally through the microscope' (Mabberley, 1985: 398). As one reviewer of Mabberley's book for a general readership remarked (*Times Literary Supplement*, 11 April 1986: 400): 'It is sad that such a man [as Robert Brown] should have been so thoroughly elbowed out of history by the Bankses and Hookers'.

Our Brownian Memorabilia

Robert Brown has never been elbowed out of the history of The Linnean Society of New South Wales even though he was dead sixteen years when the society began. Not

only do we of this society share Brown's concern for science as knowledge but his friends, who were also ours, have left us a rich legacy of tokens of the man and his works. No non-member received prouder recognition than Robert Brown during this society's centenary in 1974 and now at another season of commemoration — a bicentennial purpose I prefer to mere celebration — there is added reason to remember at least some of his tokens.

The year 1988 indeed marked not only the bicentenary of anglophone Australia but also of the founding of The Linnean Society of London, in a way the parent of all such bodies. Choice of an 'active' motto for our society may have followed its example: *Naturae discere mores* (to learn the ways of Nature), though the London society's decision after a

Fig. 1. Robert Brown. Engraved after the portrait by H. W. Pickersgill presented to Brown in 1835 on behalf of subscribers (among them Alexander and W. S. Macleay). The print, a gift from The Linnean Society of London to mark the centenary (1974) of The Linnean Society of New South Wales, is now on loan to the Macleay Museum which also holds on loan the society's (incomplete) collection of coloured plates from Bauer (1813). Photograph by courtesy of Lydia Bushell, Macleay Museum.

few decades of its existence to abandon interest in inorganic Nature (Linnaeus's mineral kingdom) has never had much influence with us. Nevertheless, there are treasured links between the two societies and I take this opportunity to congratulate The Linnean Society of London on its achievements over two hundred years (Gage and Stearn, 1988); may it continue to thrive. Acknowledgment of the London society raises thought here particularly of the Macleays (Fletcher, 1921; 1929) and their friends, among them Robert Brown. Brown, in fact, became an associate of the society in November 1798 only a few months after Alexander Macleay [1767-1848] had been elected its secretary, a post he was to hold until 1825 when appointment as colonial secretary of New South Wales required his retirement. Friendship between Brown and the Macleay family blossomed after his return from Sydney in 1805 and employment by the Linnean Society (Mabberley, 1985: 132), employment which continued with some change of duty until 1822. So close indeed did the friendship become during those years that Mabberley (1985: 242) thinks it 'likely' Brown and Frances Leonora (Fanny) Macleay, later Harington [1793-1836] Macleay's eldest daughter and a gifted amateur painter of flowers, were engaged to marry 'since 1815'. Windschuttle (1988: 58), however, claims Fanny Macleay had to reject Brown's suit about that time under pressure from her mother. Whatever the circumstances, the two remained close friends even after Fanny and her family removed to Sydney. From comment made in 1837 (Mabberley, 1985: 242) — by which time Fanny was dead, after only six weeks of marriage — it seems Mrs Macleay had come to regret earlier opposition to Brown as son-in-law. But by then it was too late; Brown stayed a bachelor. He also maintained his connection with the London society, occupying its presidential chair 1849-53 — the only former employee to have achieved such rank in the society's history.

The Linnean Society of London acknowledged these cherished connections in a gift to our society at the time of the centenary in 1974 — a copy of the print engraved by Charles Fox [1794-1849] and issued in 1837 after the portrait of Robert Brown painted by H. W. Pickersgill [1782-1875]. So apt was the gift (Fig. 1) it had a place of honour in the exhibition mounted by the State Library to mark our centenary (Vallance, 1975: 202-3). I may add, parenthetically, the present we sent last year for the London society's bicentenary relates activity by the collector George Caley [1770-1829] during the time Brown was also busy in the colony: one of an edition limited to 400 copies of '*The Devil's Wilderness* George Caley's Journey to Mount Banks 1804', edited by my friend and colleague on council Alan Andrews (Caley, 1984). But to return to the portrait shown here in 1974. It was, if anything, even more significant as a gift to us and to Australia than I then knew. As Mabberley (1985: 312, 395) explains, Pickersgill's painting, owned by the London society, was a subscription work paid for by Linnean fellows — Alexander Macleay and his son William Sharp Macleay [1792-1865] being among the subscribers — and presented to Brown in 1835 by George Bentham [1800-1884], later of *Flora Australiensis* (1863-78) fame. And the illustration under Brown's left arm in the portrait is that by Ferdinand Lucas Bauer [1760-1826], Brown's artist colleague in Australia, of *Brunonia australis* Sm., Brunoniaceae, the Australian plant named in Brown's honour by J. E. Smith [1759-1828], 'institutor' of The Linnean Society of London, though by accident of publication Brown himself appears to have started the name in print (Brown, 1810: 590).

An even more remarkable link with Brown and Australia came into our society's possession more than a century ago, Brown's own copy* of the account (Flinders, 1814) of the voyage which brought him to this country. The gift was received 31 August 1887 without fuss and, indeed, few people seemed to know of its existence until I exhibited the work at a meeting during the centenary year (Vallance, 1975: 203). At the time I was aware only that the donor had been described by Brown as his 'Relation & Friend'. Now,

thanks to Mabberley (1985) and the prompting of a lady in England who not only shares the botanist's surname but also descent from John Brown [d. 1701] of Angus and who was interested to learn if the family persisted in Australia, I am able to expand the story. The inscription on the half-title leaf of the first volume of our Flinders (Fig. 2) records Brown's gift of the book to John Sangster. Nor was this the only part of Brown's property Sangster received. Both he and his sister each had legacies by the will Brown signed on 19 January 1858, where Sangster is described as 'at president [sic?] resident in the Colony of New South Wales' (Mabberley, 1985: 440). Mabberley indeed suggests the brother and sister were then the only surviving close relations Brown had. As the will indicates, Brown knew their father, and his first cousin, Commander Robert Sangster R.N., was already dead.

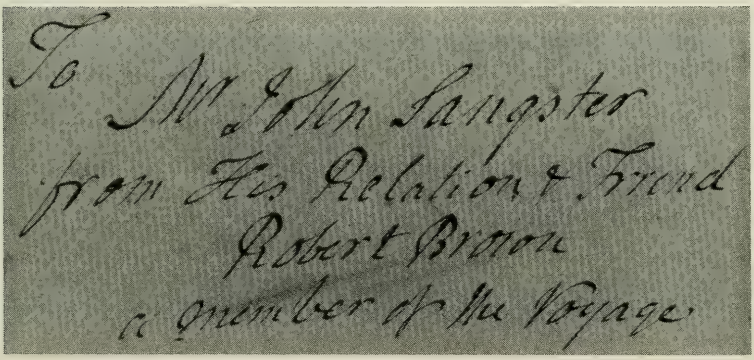


Fig. 2. Presentation inscription in Robert Brown's copy of Flinders (1814). The copy was given to The Linnean Society of New South Wales by Brown's cousin, John Sangster, in 1887; it is now on loan in the Rare Books division of the University of Sydney Library.

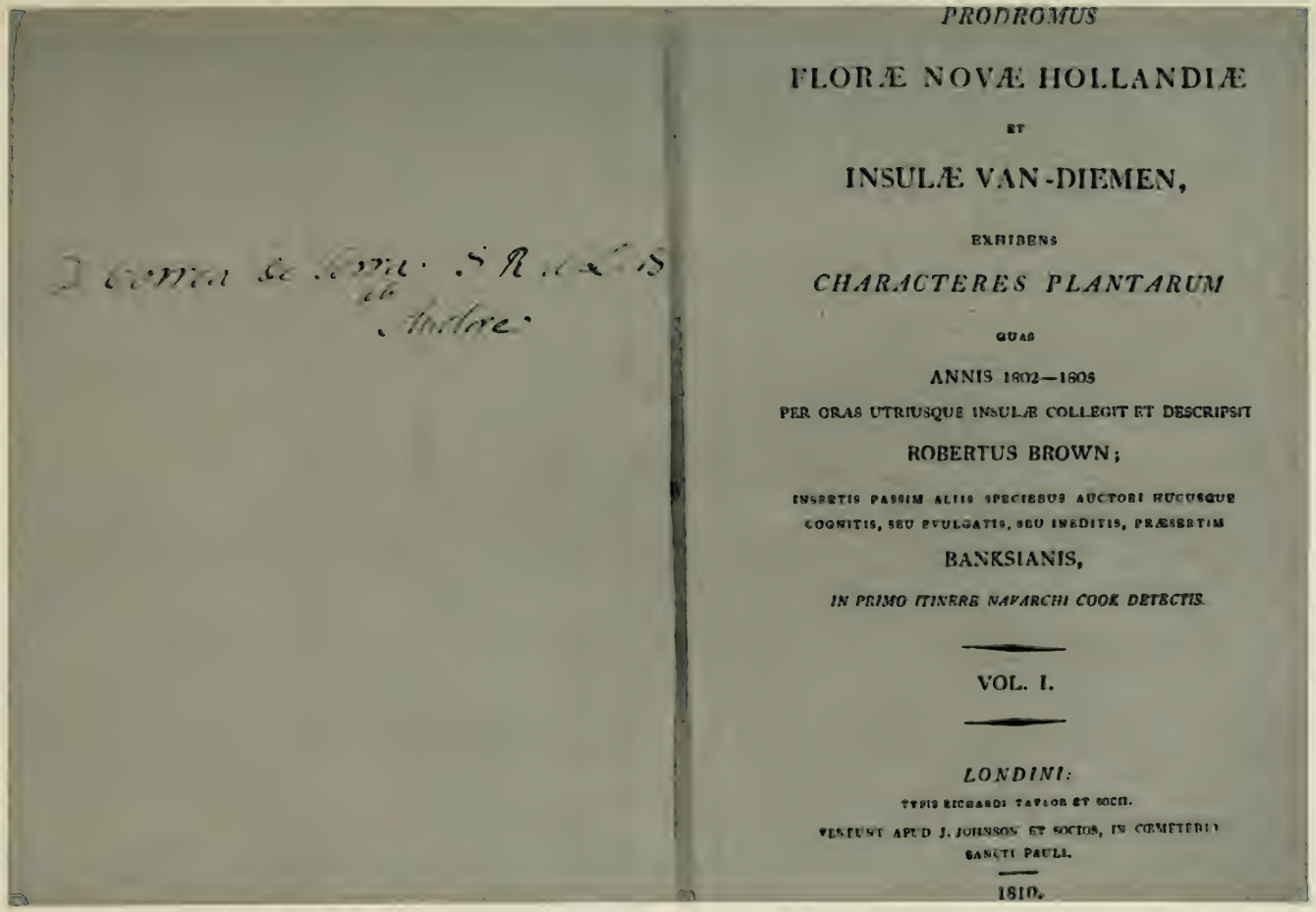
What then of this John Sangster who followed his illustrious cousin to New South Wales and in 1887 entrusted his prized relics to the care of our society? And prized by him they certainly were. Before parting with them Sangster took the trouble to set the provenance beyond doubt by making the Statutory Declaration pasted below Brown's inscription: 'I John Sangster of Sydney New South Wales do hereby solemnly and sincerely declare as follows: that the above is the handwriting of the late Robert Brown, and

* It is interesting to note in Nicol the publisher's accounts (Ingleton, 1986: 422) reference to sets 'not paid for' of the cheaper, 'Small Paper' edition assigned to 'Mr Aken' and an otherwise-unknown 'Mr Brine'. In the case at least of Aken, whom he had no trouble identifying, Ingleton was ready to admit fault while arguing extenuation: 'clever Aken never paid Nicol for his copy, which, after all, seems fair justice in the circumstances'. 'Fair justice', equally, would have embraced Robert Brown, in my view, the 'Mr Brine' of the publisher's clerk. Both Aken and Brown served Flinders loyally during the voyage and during preparation of the book, to which in fact Brown contributed an appendix. It would have been in character if the dying Flinders, expecting his two supportive companions were not grand enough to win presentation copies from the Admiralty, had urged they receive copies 'not paid for' by them. I find no convincing reason to accuse either Aken or Brown ('Brine') of deliberately avoiding payment for the work of their lamented friend.

that he gave me the book in two Volumes'. The signed declaration was witnessed 19 February 1887 by one Edward Gell J.P. It may be added the two volumes, without the Atlas which Brown may have used to destruction or kept with his collections in London, are notably free from annotations. They came into the society's hands through the agency of a lawyer and politician, L. F. Heydon [1848-1918], who it turns out was more than a mere conduit. Heydon had been elected a member of our society 28 April 1886. He thus knew the society's purpose but, more to the point, he was in a position as one of the family to explain that purpose to Sangster. It appears that Heydon was son-in-law to Gell, the witness to Sangster's declaration, and from what I make out Gell had married a sister of Sangster's wife. I have no doubt it was Heydon who convinced Sangster he should fix his gift on The Linnean Society of New South Wales.

John Sangster appears to have come to New South Wales early in the 1850s and to have served with the Royal Marines, though whether here or elsewhere, or both, is not clear to me. He could have received the gift from his cousin before leaving for Australia, when they discussed — as I assume they did — a destination Brown had known so many years earlier. If, however, the '1857' pencilled below the inscription betokens year of acquisition then either Sangster returned to London for a while or the books were sent out to him. The books are not mentioned in Brown's will, where Sangster is noted as resident in New South Wales, so these remarkable association copies must have been in this country no later than 1857. It is not clear to me what Sangster was doing at the time and the occupation 'householder' committed to the certificate of his marriage at Bathurst in 1860 to Sarah Haselden (or Haseldon) reveals little. Later, at least, Sangster had employment in what seems a clerical capacity with the N.S.W. Lands Department. It was as a pensioner of the government that John Sangster died, aged 74, at Darlinghurst, Sydney, on 1 March 1899. By then he was a widower (Sarah Sangster died 21 July 1897), cared for it seems by members of the Gell family; there were no children of his marriage. Although the Sangsters had married according to Roman Catholic rites, John Sangster remained an Anglican and was buried thus in Waverley Cemetery. The Brown family connection with Australia thus lies fixed within the nineteenth century — Robert Brown had his first sight of it, Cape Leeuwin, on 6 December 1801 — and we have a precious memento of that connection.

Our society's heritage from the Macleays has been explored in some detail by J. J. Fletcher [1850-1926] who, curiously, found little to say about Robert Brown (Fletcher, 1921: 578). He could report only 'four reprints of papers by Robert Brown with inscriptions to Alex. McLeay, Esq.' in the society's library and notice the name *Macleaya* erected for a genus of extra-Australian plants by Brown in 1826. There are, in fact, more than that number of 'reprints' — a misleading term — in what remains of our library after recent regrettable events, nor are all the Brown items presentation copies to Alexander Macleay. For instance, our copy of Brown's botanical appendix (Brown, 1826a; Linn. Soc. N.S.W., Tracts X.P.18) to Denham and Clapperton's *Narrative of Travels and Discoveries in Northern and Central Africa* . . . (1826), in which *Macleaya* R.Br., Papaveraceae, was introduced to commemorate 'my much valued friend Alexander Macleay, Esq. Secretary to the Colony of New South Wales, whose merits as a general naturalist, a profound entomologist, and a practical botanist, are well known', was a present to W. S. Macleay 'from his sincere friend R Brown'. There can be no doubt Alexander also received a copy — that sent to his son in Cuba was hardly accessible to him — but it like so much else of Alexander Macleay's library was sadly dispersed. Among items known to have been in the older Macleay's collection was a copy of Brown's first major work, his *Prodromus* on the Australian flora (Brown, 1810). Stearn in his introduction to the facsimile edition of the *Prodromus* (Brown, 1960: xxx) notes that Macleay was among the first of Brown's friends to receive a copy. But Alexander Macleay fell on hard times in the 1840s and was



PRODROMUS

FLORÆ NOVÆ HOLLANDIÆ

ET

INSULÆ VAN-DIEMEN,

EXHIBENS

CHARACTERES PLANTARUM

QUAS

ANNIS 1802—1805

PER ORAS UTRIUSQUE INSULÆ COLLEGIT ET DESCRIPSIT

ROBERTUS BROWN;

INSERTIS PASSIM ALIIS SPECIEBUS AUCTORI HUCUSQUE COGNITIS, SEU EVULGATIS, SEU INEDITIS, PRÆSERTIM

BANKSIANIS,

IN PRIMO ITINERE NAVARCHI COOK DETECTIS.

VOL. I.

LONDINI:

TYPIS RICHARDI TAYLOR ET SOCII.

VENEUNT APUD J. JOHNSON ET SOCIOS, IN COEMETERIO SANCTI PAULI.

1810.

Fig. 1. Title-page of Brown's *Prodromus* with facing presentation inscription to J. F. Correia de Serra. The volume is now on loan in the Rare Books division of the University of Sydney Library.

forced to realize various assets. The printed catalogue (John Blackmore, auctioneer, Sydney, sale 1, 2, 3 April 1846) of Macleay's library 'of nearly 4000 volumes', known only by the copy in the Mitchell Library, Sydney, is a dispiriting record. Somewhere, I hope, the Macleay copy of *Prodromus* remains, in careful hands. When, at last (the time is unclear as the copy lacks stamps*), the society acquired its copy (Fig. 3) it did almost as well — with one of the nine copies Stearn reports as sent to Paris in 1810, the one destined for J. F. Correia de Serra [1750-1823]. It was Correia de Serra who, in October 1798, introduced Brown to Sir Joseph Banks as a very good naturalist willing to go to New South Wales (Mabberley, 1984: 41).

Alexander Macleay's copy of the first, and only, supplement to the *Prodromus* (Brown, 1830) somehow escaped the dissolution of his library. It remains in a bound volume (Linn. Soc. N.S.W., Tracts X.P.12) with other notable Brown items, most of them assuredly not 'reprints'. Thus we have a copy of the first account of what is now termed Brownian Motion or Movement (Brown, 1828), printed at the author's expense and antedating publication in a journal (Mabberley, 1985: 271). With it is the at least equally rare *Additional Remarks on Active Molecules* (1829) which Brown also first had printed privately (Mabberley, 1985: 272). These are followed by a presentation copy of Brown (1831) which, as Mabberley (1985: 294) shows, was printed for the author before he read the work in two stages to The Linnean Society of London. Then there is the single leaf, lacking a presentation inscription but with a correction in Brown's hand, entitled *Additional Remarks on the Pollen Mass in Asclepiadeae* and of which a copy was sent to F. L. Bauer on 22 November 1831 (Mabberley, 1985: 294). This bound volume also contains Brown's work on *Kingia* R.Br., Xanthorrhoeaceae, which Ferguson (1941: 373, no 1003) noted as held in this country only by the National Library, Canberra, and ascribed to the year 1825. As the title-page indicates, the contribution was read before the Linnean Society in November 1825 but the slightest familiarity with that society's publications would have revealed Ferguson 1003 has another source. It comes in fact from King (1826) where Brown's essay appears in vol. 2 (pp 534-65). The separate issue we and the National Library have may be a 'reprint' but it is one with its own pagination and signatures. King's volumes were reissued in a 'main' edition in 1827, after the printer had trouble with a noble neighbour and had to retreat elsewhere (Clowes, 1953: 21-4; Common and Moulds, 1973), but there can be no doubt Brown on *Kingia*, Ferguson 1003, was printed with the 1826 issue of King. Colleagues had copies of the *Kingia* work from Brown in 1826 (Mabberley, 1985: 250) and the paper of various origins used for printing the folding plate in the several examples of Brown (1826b) I have inspected matches the diversity in King (1826). The printer appears to have had more orderly stock for the 1827 reissue but, of course, Brown needed no separates from it. The only other 'reprint' associated with Brown in our Tracts X.P.12 is of a paper on the natives of King George Sound, Western Australia, (Nind, 1831), to which Brown contributed the introduction, at least. Our copy bears Alexander Macleay's name, probably in Brown's hand. The work has its own pagination and signatures and may well be unique in Australia; there is no record of it in either Ferguson's *Bibliography of Australia* or the *Addenda* to Ferguson issued by the National Library of Australia in 1986.

Finally, as a sign of how Brown kept distant friends informed I mention our copy (Linn. Soc. N.S.W., Tracts X.P.5) of Paris (1838) inscribed 'Alexander MacLeay Esqr from his affectionate friend R Brown'. The subject of Paris's biographical sketch, W. G. Maton [1774-1835], had been closely associated with Macleay at the Linnean Society, and with Brown. By 1838 Brown's dearest friend among the Macleays was dead but his

* Further search reveals it was one of more than 700 volumes donated by Sir William Macleay in 1889 (*Proc. Linn. Soc. N.S.W.* 4, 1889: 1319).

thoughtful communication with the family to whom we owe so much continued. On 7 August 1848 it fell to Alexander's third son, George Macleay [1809-1891], to inform Brown by letter of his late father's 'most affectionate dying remembrances to his dear friend Robert Brown' (Mabberley, 1985: 378). Members of The Linnean Society of New South Wales, heritors of the Macleays, indeed have special reason to esteem *Jupiter Botanicus*.

Robert Brown in Australia

The name Robert Brown may mean little to most Australians but every systematic work on Australian plants is likely to abound with genera and species identified with the initials R.Br. That at an obvious level is a measure of Robert Brown's lasting contribution to knowledge of the Australian flora, a contribution begun with his own collecting in the field of many of the taxa still bearing the names he gave them. But whereas botanical systematists know his legacy it seems few are more than generally aware of where Brown went in this country, where he collected. It is this aspect of Brown's activity in Australia I now wish to pursue. Geologists, perhaps more than their fellow students of Nature, bother about locations, where significant specimens were collected and what the relationship was with their original surroundings. Yet locality detail is also of importance to those concerned with identity and diversity among plants and animals, detail in particular relating to places where type material was gathered. Geographical localization of Brown's plant types, and not only his, has long been a problem, for instance, for botanical systematists. The synopsis of Robert Brown's travels in Australia which follows is offered in the hope it will be of service to such specialists and, indeed, to others involved in the study of Australian Nature during early colonial times. If thereby the activity of a notable figure in our history comes to be better understood and appreciated my purpose will have been well served.

The valuable work of Mabberley (1985) absolves me of need to dilate on the circumstances of Brown's life and achievements. Suffice it to say here, that in December 1800 Sir Joseph Banks remembered the young naturalist introduced to him by letter from Correia de Serra in 1798 (Mabberley, 1985: 62). Matthew Flinders [1774-1814] had then recently returned from New South Wales with a proposal to run a hydrographic and natural history survey of the Australian coasts. The plan, apart from Flinders's wish to have Mineralogy included (Vallance and Moore, 1982: 3; Vallance, 1986: 157), gained Banks's support and before 1800 was at an end the Admiralty had commissioned a vessel as H.M.S. *Investigator* with Flinders in command. It was at this stage Banks remembered Brown and, acting for the Admiralty without saying so, offered the young Scot, then surgeon's mate with a regiment in Ireland, the post of naturalist to the expedition. Brown accepted promptly and soon was in London preparing for the adventure of his life while arrangements to secure release from his regiment dragged on. These settled, there were other delays before *Investigator* eventually got underway for Australia on 18 July 1801.

Although employed by the Admiralty, Brown's duties and priorities as naturalist were largely set for him by Banks. Botany had to be his overriding purpose but, as opportunity allowed with no penalty to Botany, he might also attend to matters of Zoology and Geology (Vallance and Moore, 1982: 3-5). In the event Brown managed reasonably across the spectrum of Natural History while more than satisfying Banks's inclination. Three assistants chosen by Banks shared in the work: the botanical artist Ferdinand Bauer, the gardener Peter Good [d. 1803] who was to look after plants destined for Kew, and a 'practical miner' from Banks's Derbyshire estates, John Allen [*c*1775-1869?], in the company perhaps as a sop to the commander. For a recent account

of the voyage, and of Flinders, the reader should consult Ingleton (1986). But travel with Flinders covered only part of Brown's time in Australia. While in the Gulf of Carpentaria in November 1802 Flinders was advised his ship might last another six months at sea, barring bad weather or accident. With skill and fortitude he brought *Investigator* back to Sydney (9 June 1803) by way of Timor, but at a cost. Some had died on the voyage from Timor, others were seriously ill, among them the commander. Peter Good survived the journey only to die on the third day after arrival.

The period from 9 June 1803 was as critical for Brown as it was for Flinders. *Investigator* became a hulk in Sydney Harbour and, when Flinders resolved to return to London in the hope of securing a replacement vessel to complete his survey terminated off Arnhem Land, Brown and Bauer sought and were granted permission to remain in the colony to extend their work. Allen at first proposed to stay with his colleagues but changed his mind (Vallance and Moore, 1982: 30-1) and sailed on *Porpoise* with the landscape painter William Westall [1781-1850] and the rest of *Investigator*'s company. It was Allen who, after reaching England by way of China in August 1804, brought first-hand news to Banks of Good's death, of the fate of *Investigator*, of the wreck of *Porpoise* and the rescue of its people but not of the plants Brown entrusted to it.

Brown and Bauer continued their activity in Australia, sometimes together sometimes going their separate ways, for almost another two years. During that period Brown visited Tasmania and the Hunter River area and Bauer spent six months at Norfolk Island. Finally, and much against Brown's wishes, the two men joined a resuscitated *Investigator* which left Sydney 23 May 1805 on a non-stop voyage to England by way of Cape Horn. Furthermore, the leaky, once-condemned vessel completed the journey without mishap, reaching Liverpool 13 October 1805. But that was not the end of Brown's trials. The commander of *Investigator* failed to clear the contents of his ship with Customs before going off to London. Brown and Bauer had to wait at Liverpool, urging Banks and his factotum librarian Jonas Dryander [1748-1810] by post to expedite clearance of the collections. Not until 5 November 1805 did Brown and Bauer see London again; they had left it for Portsmouth 14 June 1801 at the start of a remarkable journey which turned out to involve not merely circumnavigation of Australia but of the world.

As Brown informed Banks by letter 19 October 1805 it was a considerable cargo which delayed him and Bauer at Liverpool. Apart from five boxes or packages of clothes and two with miscellaneous contents, there were 11 of drawings of all sorts, 12 of dried plants, two of 'Birds & Beasts Preserved', one of insects and three (elsewhere* Brown makes it four) of 'Minerals'. Mabberley (1985: 128-31) outlines some of the contents: 3600 plant specimens from Australia, '3200 being different, 200 from Timor; 23 mammals, 217 birds, 39 fish, 33 reptiles and amphibians and 29 invertebrates other than insects. Of the animals, according to Mabberley, 'none but the birds and insects was ever worked on systematically'. Banks, to whose house the whole collection had been delivered, simply handed the 'Minerals' over to the Admiralty, the real owner of all the natural history material including drawings, whence they went to the British Museum (Vallance and Moore, 1982: 10). The month after his return to London Brown took up employment with the Linnean Society but was able to continue working on his plants at Banks's house under Admiralty auspices. Banks, indeed, managed to have that financial support maintained until 1811 (Mabberley, 1985: 177), by which time Brown had published his *Prodromus*. The plant collection brought back on *Investigator* may not have matched in number that returned on *Endeavour* in 1771 (Beaglehole (1974: 273) claims Banks and Solander had 17000 plants) but Brown made vastly more for science with his.

* Brown Correspondence, vol. 3: 125; BM(NH) Botany Library.

My serious interest in tracking Brown in Australia had its origin in Edwards (1976), a paper which for the first time in print supplied detail of what remained in the British Museum (Natural History) of Brown's rock and mineral collection. Some of the cited localities made no geographical sense. The source of the difficulty became clear in 1978 when I had the opportunity to examine the material with which, fortunately, Brown's original paper slips had been preserved. Whoever registered the specimens (in the 1890s) was ignorant of the geographical notation devised by Flinders and used by Brown in the field (Vallance and Moore, 1982: 10). Whether botanists were then aware of the system I do not know but the publication by Burbidge (1956) of a key apparently passed without notice in the Minerals Department, BM(NH). The task of correcting registration of Brown's rocks led my colleague David Moore and me to consult Brown's manuscript Diary in the museum's Botany Library. We found, with some effort, the execrable handwriting could be read. So it was after work on the rocks was completed, and aware that hitherto only a few fragments of the Diary had been published, we decided to attempt a complete transcription in collaboration with Eric Groves, formerly of the Botany Department, BM(NH). The venture, with explanatory notes, is now almost complete, in a state of final revision before hoped-for publication.

Brown's Diary, of course, is an essential aid to following his travels in Australia yet it is also an imperfect one. Not only is it an incomplete record but in places there are problems, notably with dates. Some of Brown's dated specimen slips are likewise not free from error. Evidently at times the naturalist forgot his calendar and entering remarks some while after the event, as he occasionally did, was one source of confusion. During the voyage with Flinders, Brown's lapses as a rule are easily repaired, by means of the ship's log, Flinders (1814) and, especially, Good (1981). The journal kept by the gardener Peter Good and now available in the edition by P. I. Edwards [1916-1984] is an impressive source though the reader perhaps should be warned of the following errors in the printed text: the entry for 22 July 1802 (p. 82) continues on p. 96 after the third word of the fourth line of the entry for 29 October 1802, the text following on pp. 96-7 relates to the matching days in July (not October) as far as '7PM' on line 8 of the entry for 28 October (i.e. July) on p. 97, but the next three lines in fact complete the entry for 29 October (p. 96). It is all very confusing unless one has access to the original manuscript. Bauer and Allen appear not to have kept journals, though the annotations to Bauer's paintings can serve as useful indicators of time and space.

After Good's death, and the separation from Flinders and the ship, the task of establishing where Brown went becomes vastly more difficult, and more open to error. It is not surprising Burbidge (1956) confined her list (alas, also not without mistakes though it is quoted verbatim by Stearn in Brown, 1960: xxi-xxiv) of Brown's collecting localities to those visited from *Investigator*. Yet they relate to activity during roughly half the time Brown spent in this country. The period June-November 1803 when Brown was based in Sydney is quite without any Diary record. To get even an impression of what was done then one must depend on miscellaneous sources, the local weekly newspaper, letters, and original labels with Brown's herbarium specimens and Bauer's paintings. The Diary was resumed when Brown put to sea (November 1803) for what he expected to be a short visit to Bass Strait and Port Phillip but became an extended stay in Tasmania. The founding of Hobart while he was there passed him by; he was too busy in the field. Fortunately, on some of his Tasmanian excursions Brown had companions who kept records, the chaplain Robert Knopwood [1763-1838], and the mineralogist A. W. H. Humphrey [*c*1782-1829]. Humphrey, in particular, is a useful adjunct (Vallance, 1981: 132-40). But for much of his time in Tasmania there is only Brown's record which became increasingly scrappy and lapsed before he was due to return to Sydney in August 1804. Back in Sydney, Brown learned as we do from the newspaper that Bauer

had left for Norfolk Island only days before. Again, Brown forgot the Diary, except for notice of a visit to Caley at Parramatta, until 9 October 1804 when he embarked for the Hunter River and what is now Newcastle. The Diary ends 4 November 1804, with Brown up the Paterson River which, by quirk of history, he knew as the Williams. It should be recognized that in Brown's time what is now the Hunter River above Raymond Terrace was the Paterson, our Paterson was the Williams and the Williams was known as the Hunter. Herbarium slips and shipping records point to Brown's return to Sydney 20 November 1804. From then until he left our shores six months later there are only scattered sources to guide the seeker after Robert Brown in Australia.

What follows as a calendar of Brown's travels in Australia derives from the efforts of Groves, Moore and myself though as the only Australian in the team I must accept responsibility for what errors of geographical interpretation are found therein. The work is imperfect, after all the original record is far from complete, but at least Brown can now be followed well beyond where Burbidge (1956) left him. The maps shown during presentation of this address are being held for the edition of Brown's Diary; it is hoped, however, that modern place names and geographical coordinates given in the calendar will serve for readers having access to standard topographical maps. Where no name is attached to some record of activity in the calendar, Brown's involvement may be assumed.

Calendar of Robert Brown's Activity in Australia

8 December 1801–5 January 1802 King George Sound, Western Australia (King George III[d]s Sound of Brown and the discoverer, George Vancouver [1757-1798], in 1791

Anchorages: (1) off Seal Island, 35°05′S, 117°58′E (8.xii); (2) entrance to Princess Royal Harbour (10.xii); (3) off N shore Princess Royal Harbour (12.xii); (4) off Seal Island (3.i).

Shore work: on Flinders Peninsula, towards Bald Head (9.xii, Good got off that night but Brown, Bauer and Allen to a.m. 10.xii) — Vancouver Peninsula (10.xii, Good only) — vicinity of Mt Martin, entrance to Oyster Harbour (11.xii) — Mt Clarence (35°01′S, 117°54′E), N side Princess Royal Harbour and within present Albany town area (12, 13.xii) — N shore Princess Royal Harbour (14, 21, 27.xii, Good also visited there on other days to get soil and plants for his garden) — meeting with aborigines, N shore Princess Royal Harbour (15.xii) — walk from Emu Point along W shore Oyster Harbour to King River, up river *c*4km and return across country, night spent by Lake Seppines (17-18.xii) — walk to coastal hills from SW shore Princess Royal Harbour (20.xii) — walk, with Flinders and others, to Torbay Inlet, night spent near Lake Powell, and return by the coastal hills (23-24.xii) — Vancouver Peninsula (28.xii, Brown and Allen) — study of aborigines, opposite anchorage (30.xii, Brown with Bell the surgeon) — vicinity of Limeburner Point, S shore Princess Royal Harbour (31.xii, with Flinders and others, not Good) — again to Limeburner Point but for walk E to King George Sound (1.i, Brown and others, not Good) — as for 1.i (2.i, Good only) — Flinders Peninsula, about Isthmus Hill (4.i, later in the day Brown visited Seal Island with Flinders).

9–14 January 1802 Lucky Bay, Western Australia (Bay I or 1 during the voyage)

Anchorage: within Lucky Bay and *c*1.5km WSW of Mississippi Hill.

Shore work: Mississippi Hill (33°59′S, 122°16′E) and vicinity (10.i) — Thistle Cove and vicinity (11.i) — about landing place Lucky Bay, Brown and Allen/towards

Frenchman Peak (33°58′S, 122°10′E), Good only (12.i) — to summit Frenchman Peak (13.i).

14–17 January 1802 Goose Island Bay, Archipelago of the Recherche, Western Australia (Bay II or 2 during the voyage; Brown also referred to Middle Island as 'Island No 2')

Anchorage: in passage between Goose and Middle islands, at W entrance to Goose Island Bay.

Shore work: on Middle Island, in particular its E part and the salt lake, Goose Island (34°05′S, 123°11′E) visited in evening (15.i) — W side Middle Island with ascent of Flinders Peak/according to Brown, Allen 'walkd round the island' (16.i).

28–29 January 1802 Fowlers Bay, South Australia (Bay III or 3 during the voyage)

Anchorage: 32°00′S, 132°27′E, in Fowlers Bay *c*5km NNW of Point Fowler.

Shore work: vicinity of present Fowlers Bay settlement and on Point Fowler peninsula (29.i, a.m. only).

2–4, 8–9 February 1802 Petrel Bay, St Francis Island, Nuyts Archipelago, South Australia (Bay IV or 4, or Anchorage IV or 4, during the voyage)

Anchorages: about 32°30′S, 133°18′E, off N side of the island.

Shore work: traverse of the island (3.ii) — Flinders ashore a.m. 4.ii but claimed naturalists were deterred by oppressive heat, and neither Brown nor Good reports landing (the claim by Black (1957: 749) that Brown this day collected *Solanum hystrix* R.Br., Solanaceae, must be doubted; a Brown specimen of the plant in the BM(NH) herbarium, however, can reasonably be attributed to 'Anchorage V') — visit, according to Brown, for 'plants gatherd sparingly when last here' (8.ii, Good only).

6–7 February 1802 St Peter Island, Nuyts Archipelago, South Australia (Anchorage V or 5 during the voyage; Burbidge (1956: 231), in error, sets Anchorage V as 'Off Franklin Isles', a place never visited from *Investigator* though some Brown plants, e.g. *Scaevola spinescens* R.Br., Goodeniaceae, Bennett 2573 in the BM(NH) herbarium, are assigned to it as collected from Anchorage V)

Anchorage: off N side Goat Island (32°18′S, 133°31′E), at its E end.

Shore work: in W and NW parts of St Peter Island on a day of summer heat during which Brown became separated from his companions/earlier in the day Bauer landed with Flinders on Goat Island (7.ii).

11–12 February 1802 Waldegrave Islands, South Australia (Anchorage VI or 6, also 'Island u', during the voyage; note error in Burbidge, 1956: 231)

Anchorage: off N side of the larger, more easterly, island (33°36′S, 134°48′E).

Shore work: walk along shore opposite ship and traverse across island (11.ii, chiefly a.m.).

12–14 February 1802 Flinders Island, South Australia (Anchorage VII or 7, also 'Island x', during the voyage; note error in Burbidge, 1956: 231)

Anchorage: in Flinders Bay, off NW shore of the island (33°43′S, 134°31′E).

Shore work: Good has 'traversed the greater part of this island'/Brown indicates a visit 'near the eastern extremity' and N part of the island (13.ii). In the Diary Brown reveals for the first time that he had here compiled a local plant list, 'Florula No VII'. It has not been traced.

20–22 February 1802 Thistle Island, South Australia (Anchorage VIII or 8 during the voyage; at first, Flinders seems to have termed it Uncertain Island)

Anchorage: near 34°56′S, 136°04′E, off NW corner of the island.

Shore work: in that part of island opposite the ship (21.ii, a.m.).

22–25 February 1802 Memory Cove, South Australia (Bay IX or 9 during the voyage but Flinders named it Memory Cove while there searching for a cutter lost 21.ii with eight lives; Brown was using the name by 3.iii.1802)

Anchorage: within the cove (34°58′S, 135°59′E).

Shore work: along coast N from anchorage *c*3km, mainly in search of survivors or wreckage (22.ii) — walk inland (W) *c*2km to summit where Brown saw Port Lincoln to NW (23.ii) — over ground covered 22.ii (24.ii, Good only; Flinders this day confirmed Brown's sighting of inlet to NW).

23 February–6 March 1802 Port Lincoln, South Australia (Bay X or 10 during the voyage)

Anchorage 1 (25.ii): inside Surfleet Point ('Cape T_1') and roughly N of Stamford Hill ('Hill T').

Shore work: for an hour in evening (25.ii) — to summit Stamford Hill, 34°47′S, 135°56′E (26.ii, a.m.).

Anchorage 2 (26.ii): at SW corner Port Lincoln Proper.

Shore work: walk with Flinders to Sleaford Mere (34°50′S, 135°44′E), in search of fresh water (26.ii, p.m.) — along shore NW to North Side Hill (27.ii) — walk *c*2km along shore E from anchorage (28.ii, Good only) — to shore of Sleaford Bay and circuit of Sleaford Mere (1.iii) — walk 'towards the bottom of' North Side Hill (3.iii) — neighbourhood of anchorage (4.iii, Good only).

Anchorage 3 (5.iii): in entrance to Spalding Cove and off Engine Point (34°45′S, 135°59′E).

Shore work: W side Cape Donington ('Cape T') peninsula, about Cape Colbert (5.iii, p.m.)

6–7 March 1802 Kirkby Island, Sir Joseph Banks Group, South Australia (Anchorage XI or 11, or 'Island $\varkappa_1$', during the voyage)

Anchorage: off N side of Island (34°33′S, 136°13′E).

Shore work: 'walkd over the greater part of the island', according to Brown (7.iii, a.m.). Brown mentioned a Florula in the Diary but deleted the passage.

9–13 March 1802 Head of Spencer Gulf, South Australia (Inlet or Bay XII, or 12, during the voyage)

Anchorage: off Red Cliff Point (32°30′S, 138°00′E).

Shore work: excursion to summit of Mt Brown ('Mount X'), Brown and party spent the night on mountain after reaching the top near dusk, their servants (who had abandoned the climb) camped by Woolundunga Creek and were reunited next morning (10-11.iii). Brown's Florula for this venture has been preserved.

21–24 March, 1/2–7 April 1802 Kangaroo Island, South Australia (Anchorage XIII or 13 during the voyage, but also Kanguroo Island of both Flinders and Brown)

Anchorage 1 (21.iii): off N coast of island, between Hog Point (Kanguroo Head of Flinders) and present Kangaroo Head. Burbidge (1956: 231) errs with regard to which side of Nepean Bay; the place is east not west.

Shore work: walk *c*2km W of landing place, 'keeping nearly the margin of the brush' (22.iii) — walk (Brown has 'about 3 miles') along coast (23.iii, Good but not Brown).

Anchorage 2 (1/2.iv): in the Eastern Cove of Nepean Bay, *c*3km SW of present Kangaroo Head.

Shore work: walk along shore to SW according to Good whose stated direction makes more sense here than that (to E) given by Brown (2.iv) — exploration of Eastern Cove and Pelican Lagoon, with visit to Prospect Hill (also known as Mt Thisby, 35°51′S, 137°45′E), Brown with Flinders/a 'ramble through the woods' E from the anchorage, Good with Westall and Allen (4-5. iv).

27 March–1 April 1802 Gulf St Vincent, South Australia (Inlet or Bay XIV or 14 during the voyage)

Anchorage (29.iii): off Mangrove Point (34°16′S, 138°01′E).

Shore work: to near head of gulf by cutter, then walk *c*4km NW to rising ground (30.iii, Brown with Flinders, not Good).

22–22 April 1802 King Island, Tasmania (Anchorage XV or 15 during the voyage)

Anchorage (23.iv): off Boulder Point (39°38′S, 144°03′E), on N coast of the island.

Shore work: about one hour (Brown) or from soon after 3 p.m. until dusk according to Flinders (23.iv, Brown with Flinders and Westall) — walk 'over the first rising ground behind the sand hills' to a freshwater lake (24.iv, a.m.).

26 April–3 May 1802 Port Phillip, Victoria (Bay or Port XVI, or 16, during the voyage; here Brown's 'South Coast' series of localities ends)

Anchorages: various off N shore of tip of Mornington Peninsula.

Shore work: by boat and foot to summit of Arthurs Seat, Brown with Flinders and Westall/walk SW from about present Sorrento to shore of Bass Strait, Good with Bauer and Allen (27.iv) — from a landing between present Rosebud and Rye, reconnaissance across Mornington Peninsula just W of ridge from Arthurs Seat to Cape Schanck (29-30.iv, Good, Westall and Bell) — vicinity of landing place 29.iv (1.v, Bauer only) — walk (a.m.) across W end of Mornington Peninsula from a landing near modern Portsea and (p.m.) visit by boat to vicinity of present Queenscliff and Swan Bay (2.v, Brown but not Good).

9 May–22 July 1802 Port Jackson (Sydney), New South Wales

Anchorage: in Sydney Cove.

Shore work: in vicinity of the town, Sydney (10.v, Good) — the same (11.v, Brown and Good with Leschenault de la Tour (Vallance, 1986: 179)) — establishing a workplace in lodgings (12-13.v, Good at least) — collecting about Sydney (14-21.v, Good at least) — seed collection brought ashore and prepared for despatch (21-25.v, Good) — collecting about Sydney (26-29.v, Good at least) — walk to Hawkesbury River and back, Windsor (Green Hills) and Richmond Hill, overnight stops en route at Old Toongabbie (Constitution Hill) (30.v-3.vi, Good; Brown wrote letters in Sydney 30.v) — collecting about Sydney (4-16.vi, Good at least), Brown, Bauer, Westall, Good and probably Allen walk to Parramatta (17.vi) — Brown's party visits North Rocks (Jerusalem Rocks) with George Caley (18.vi) — party walks from Parramatta to Castle Hill and back, again with Caley (19.vi) — Brown's party to the Hawkesbury at Green Hills (20.vi) — visit to Cornwallis Farm and vicinity (21.vi) — up river by boat to Richmond Hill, then to just above junction with Grose River and a walk towards Grose Head South, late return to Green Hills (22.vi) — down Hawkesbury by boat *c*23km to Portland Head and back (23.vi) — return from Green Hills to Parramatta (24.vi) — Parramatta to Sydney (25.vi) — 'securing former collections' and short walks about Sydney (26.vi-2.vii, Good at least) — visit to Botany Bay, Cooks River and thereabouts (3.vii) — walks to South Head and vicinity (4-12.vii, Good at least) — preparing for next stage of voyage and storing collections to be left behind (13-20.vii). On 21 July *Investigator* sailed out of Sydney Cove with *Lady Nelson* and anchored off Bradleys Head in readiness for departure from Port Jackson next day.

29 July–1 August 1802 Hervey Bay, Sandy Cape (Fraser Island), Queensland (The bay and cape were named by James Cook from his survey in 1770; Brown's East Coast series begins here and extends to Torres Strait)

Anchorage: in Hervey Bay, *c*6km NW of present Sandy Cape Lighthouse (24°44′S, 153°13′E).

Shore work: in vicinity of landing place 'near the Easternmost extremity of the sand patch', presumably then the shore almost due N of the lighthouse site (30.vii, p.m.) — from a landing place somewhat NE of that used 30.vii, Brown and party went SW past the sand patch before striking inland to SE a short way ('our very limited time not allowing us to take a more extensive walk') and returning to the boat in early afternoon (31.vii, mainly a.m.). Brown's local plant list remains.

5–9 August 1802 Port Curtis, Queensland (East Coast Port I or 1 during the voyage)

Anchorage: off the entrance to Port Curtis, between Curtis and Facing islands.

Shore work: a walk across the SE point (present Southend, 23°46′S, 151°19′E) of Curtis Island interrupted by a skirmish with aborigines in which, according to Brown, 'they seemd to have much the advantage of us in point of bravery & also in conduct' (5.viii, p.m.) — walk N towards Connor Bluff from Southend, mainly behind the beach (6.viii) — visits to Facing Island (7, 8.viii, Good and others but not Brown). The plant list 'East Coast Port I Aug^{t} 5 — 1802' remains, as does one of eight rock specimens collected here.

9–17 August 1802 Keppel Bay, Queensland (Named by James Cook)

Anchorage: off Dinky Point (22°30′S, 150°58′E), at NW corner of Curtis Island.

Shore work: in vicinity of Dinky Point (9.viii, p.m.) — about Sea Hill, 2km E of the point (10.viii) — Dinky Point (11.viii, a.m.?, Good but not Brown) — in whaleboat to explore The Narrows (an effort which fixed the character of Curtis Island), night at what is now Ramsay Crossing (12-13.viii, Flinders with Brown; meanwhile, Good, Westall and Allen walked to Cape Keppel 12.viii) — Brown and party (not including Good) went 'towards' Cape Keppel (14.viii) — Brown, Bauer and Good by boat to South Hill (23°35′S, 150°57′E), Connor Creek (15.viii) — friendly interview with aborigines on beach opposite the ship (16.viii). No plant list for Keppel Bay has been found and only one of four rock specimens remains.

21–24 August 1802 Port Clinton, Queensland (East Coast Port II or 2 during the voyage; Flinders in 1814 termed it Port Bowen)

Anchorage: within Port Clinton, *c*1km SW of Entrance Island.

Shore work: walk to a summit (near 22°28′S, 150°45′E) *c*1km NW of the mouth of Flinders Watering Gully, just inside North East Point, the N (mainland) head of Port Clinton (21.viii, p.m.) — walk to a higher summit (*c*2.5km NW of North East Point), down its NE side 'to a small sandy beach' and return 'across the hill climbd yesterday' (22.viii) — visit to Entrance Island (23.viii, Brown with Flinders, not Good). No list of plants from here has been noticed but one of five rock specimens in Brown's catalogue is preserved.

25 August 1802 Clara Group, Hervey Islands, Queensland (Brown refers to the locality as 'Harveys Islands')

Anchorage: off N side of the northernmost group (Clara Group, 22°20′S, 150°43′E) of the Hervey Islands.

Shore work: a brief visit only to the middle, and largest, of the Clara Group (25.viii, Flinders with Brown but presumably not Good).

26–28 August 1802 Strong Tide Passage, Queensland

Anchorage 1 (26.viii): in NE entrance to the passage, *c*1.5km W of Reef Point.

Shore work: after landing on mainland beach opposite the ship, a walk *c*5km SSE to the summit of 'the highest hill' (22°22′S, 150°35′E), which Flinders was to name Mt Westall, and return (26.viii). Brown refers to the locality as 'Shoal Bay Passage'.

Anchorage 2 (27.viii): at SW entrance to the passage, and off (WNW of) Triangular Island.

Shore work: near S extremity of Townshend Island (28.viii). Brown terms the place 'Cape Townshend Island'.

29 August–4 September 1802 Shoalwater Bay, Queensland (Shoal Bay of Brown)

Anchorage 1 (29.viii): well out in the bay, *c*8km roughly W of Triangular Island and some 10km from the S shore.

Shore work: from a landing near Sabina Point (22°24′S, 150°18′E) on the S shore (after a long haul by boat) a walk SW ('3 miles') towards N end of Normanby Range, Rocky Creek discovered before return to ship (30.viii).

Anchorage 2 (2.ix): near S shore, roughly midway between Sabina Point and E end of Akens Island.

Shore work: walk from a landing place *c*4km W of Sabina Point on a WSW course to Pine Mountain ('Peakd Hill' of Brown), 22°26′S, 150°12′E, but being late off the mountain the party camped near junction of Charcoal and Ross creeks before returning to the beach next morning (3-4.ix).

5–8 September 1802 Thirsty Sound (eastern end), Queensland

Anchorage: in E entrance to the sound, *c*1km S of Pier Head (22°07′S, 150°02′E).

Shore work: on Pier Head, Bauer with Flinders/on mainland opposite, about Arthur Point, Good and others but probably not Brown (5.ix) — 'at the bottom of Pier head', Brown (6.ix). Among material assigned by Brown to 'Thirsty Sound, entrance' is a specimen (BM 75792) in the rock catalogue as from 'Island B'. Flinders, with Westall, visited the place 6-7.ix and named it the 7th Northumberland Island (now, Tynemouth Island). It is not known if they also brought back plants for Brown. Brown's work about the W entrance to Thirsty Sound is noticed under *Broad Sound*, anchorage 4.

8–28 September 1802 Broad Sound, Queensland

Anchorage 1 (8.ix): in Broad Sound, *c*5km SE of West Hill Island (21°50′S, 149°29′E).

Shore work: on the island, then thought to be a promontory ('West Peakd Hill' of Brown), Brown claimed to have reached the top but Flinders found the brush 'too thick to be penetrable' (9.ix, a.m., Brown with Flinders, Bauer and Westall).

Anchorage 2 (10.ix): *c*2km WNW of Flock Pigeon Island (4th Flat Island of Flinders), 22°08′S, 149°35′E.

Shore work: Brown 'walkd from one end of the island to the other' in two hours (10.ix, Brown, with Flinders, Bauer, Westall and Bell). The place is noticed as 'Broad Sound Low Island' by Brown.

Anchorage 3 (12, 13, 25.ix): *c*1.5km off Upper Head (22°25′S, 149°49′E), near Charon Point on the SW shore of the sound.

Shore work: vicinity of Upper Head (12.ix) — in *Lady Nelson* and then whaleboat up the sound into Herbert Creek, from this on 15.ix a walk *c*5km SSW to The Brothers (22°41′S, 150°00′E) and back, return to Upper Head in whaleboat (14-17.ix, Brown with Flinders), meanwhile, a walk from Upper Head S towards Cliff Peak, night 14.ix spent near Bald Hills (perhaps also that of 15.ix on the return) (14-16.ix, Good with Bauer and Allen) — vicinity of Upper Head (18.ix, Good) — [move to anchorage 4] — walk from Upper Head to a 'very considerable rivulet' (then dry) draining from Cliff Peak to the Styx River, over country seen earlier by Good, Bauer and Allen (25-26.ix). The locality is 'Broad Sound — Upper head' in Brown's rock catalogue.

Anchorage 4 (20.ix): *c*1.5km W of Mangrove Islands, near SW entrance to Thirsty Sound.

Shore work: on 'a very small Island', now termed Bluff (22°16′S, 149°53′E) (20.ix) — on an island (22°17′S, 149°55′E) with red cliffs, at the opposite (mainland) side

of the sound (21.ix) — on another (cf 20.ix) of Mangrove Islands (a.m.) and then at Island Bluff (22°19′S, 149°55′E) (23.ix, perhaps not Good). Brown referred to these places as 'Broad Sound — inner entrance to Thirsty Sound'.

28 September–4 October 1802 Percy Isles, Northumberland Isles, Queensland (Northumberland Islands during the voyage, later Percy Isles of Flinders)

Anchorage (29.ix): off West Bay of Middle Island and roughly E of Pine Island (21°40′S, 150°13′E).

Shore work: about 2 hours on Pine Island, a.m. Brown/on Middle Island, p.m. Good (29.ix) — on Middle Island, walk to top of 'Pine Gully' behind West Bay (30.ix) — by boat to South Island, landed (probably at Rocky Shelf Bay) and climbed hill nearby, sailed round the island and back to ship, Brown with Flinders/on Middle Island with plant boxes for soil, Good (2.x) — visit to Pine Peak Island, Bauer with Flinders/final collecting visits to Middle Island (Good) and a.m. to Pine Island (Brown) (3.x). In the Diary and rock catalogue Brown refers to Pine Island as 'Small Pine Island'; the other 'Northumberland Islands' are there identified according to size, shape and/or position. When in 1814 Flinders distinguished this group as the Percy Isles, the present Middle Island was denoted (Island) No 2, South Island was No 1 and Pine Peak Island was No 3. Other members of the group were not visited in 1802.

5–14 October 1802 Great Barrier Reef, Queensland

Anchorage (9.x): 20°51′S, 151°04′E.

Landing: from boat on Rip (also Riptide) Cay or thereabouts to examine character of the reef (9.x, p.m., Brown with Flinders).

15–17 October 1802 Calder Island, Cumberland Isles, Queensland (Cumberland Island 1_2 of Flinders but 'Island 1' of Brown)

Anchorage (15.x): *c*2.5km NW of the island (20°46′S, 149°37′E).

Shore work: perhaps only in the NW part, Brown notes the vicinity of the steep cliffs was not examined (16.x, a.m.). On 15.x Flinders had set course for 'Island 1' (Scawfell Island, 20°52′S, 149°37′E) but tide carried the ship 'too far to leeward' causing him to fetch for the 'lesser island' 1_2.

29–30 October 1802 Murray Islands, Coral Sea

Anchorage: off N side of the largest (Maer) of the Murray Islands (09°56′S, 144°04′E).

Observations: there was no landing from the ship but natives came out to trade, Brown made notes on their physical features, vocabulary and produce (29, 30.x).

30 October 1802 Zuizin Island, Coral Sea ('Low Island d' during the voyage; Flinders later termed it Halfway Island, a name only recently displaced on maps)

Anchorage: W of the island (10°06′S, 143°19′E).

Shore work: 'walkd round the island' in about an hour (30.x, p.m., Brown with Flinders, Bauer and Westall). Brown's list of plants from this place forms part of the Diary manuscript. The locality is there given as 'Low Island' with 'Half way Island' added later; in the rock catalogue it appears as 'Torres' Strait Low Island d'.

2 November 1802 Goods Island, Torres Strait, Queensland ('Prince of Wales Island e' during the voyage; later, Good's Island of Flinders)

*Anchorage: c*2km NW of S end of the island (10°34′S, 142°09′E).

Shore work: 'ascended the hills abreast of the ship; Went down & walk'd along the beach on the other side about a mile & returnd', according to Brown (2.xi, a.m., Brown, Westall and Bell; p.m., Good, Flinders and Bauer). Brown's plant list for

'Prince of Wales' Islands Island e' forms part of his Diary manuscrupt; the same designation was used in the rock catalogue.

7 November 1802 Pennefather River, Cape York Peninsula, Queensland (Coen River of Flinders, and Brown)

Anchorage: *c*5km W of mouth of the river (12°14′S, 141°43′E).

Shore work: vicinity of two landing places on N shore of estuary *c*2km in from mouth on that side (7.xi, Brown with Flinders and Bauer). Brown's plant list for 'Gulf of Carpentaria River 3[d]' ('Gulf of Carpentaria Coen River' in the rock catalogue) is part of the Diary manuscript. The name Coen River here arose from difficulty Flinders had interpreting results of earlier Dutch exploration. Brown misdates his visit.

16 November–1 December 1802 South Wellesley Islands, Gulf of Carpentaria, Queensland

Anchorage 1 (17.xi): *c*1.5km S of Sweers Island ('(Carpentaria) Island a' during the voyage).

Shore work: on Sweers Island which 'was travers'd in various directions' (17.xi) — on Bentinck Island ('Island b') (18.xi, Good and Allen).

Anchorage 2 (20.xi): *c*3km ESE of Allen Island ('Island c').

Shore work: on Allen Island, 17°02′S, 139°14′E (20.xi).

Anchorage 3 (21.xi, adjusted 23.xi): in Investigator Road (between Bentinck and Sweers islands), S of Raft Point (Bentinck Id) and N of Inscription Point (Sweers Id).

Shore work: on Bentinck Island (22.xi) — on Sweers Island, from near Inspection Hill (17°08′S, 139°37′E) to Inscription Point (24.xi) — Sweers Island, to NE part and return (25.xi, p.m., Good perhaps with Bauer) — as for 25.xi (27.xi) — Bentinck Island (28.xi, Good). Of this anchorage Brown remarks in the Diary: 'before we left it I had made out a Florula comprehending 180 species of perfect plants'; the document has not been located. While at Investigator Road Flinders had an inspection made of the ship. He learned from the report received 26.xi 'she may run six months longer without much risk' in fine weather and barring accident.

1–7 December 1802 Wellesley Islands, Gulf of Carpentaria, Queensland

Anchorage 1 (3.xii): off SE shore of larger Bountiful Island ('Island f' during the voyage).

Shore work: on the larger Bountiful Island, 16°40′S, 139°52′E (3.xii, p.m.) — the same, 'walkd over a considerable part of the Island' according to Brown (4.xii).

Anchorage 2 (6.xii): NNW of Pisonia Island ('Island e').

Shore work: at Pisonia Island (16°30′S, 139°48′E), 'walkd round the island & penetrated into it in several places' according to Brown (6.xii, p.m., Brown with Flinders, Westall and Bell).

13–28 December 1802 Sir Edward Pellew Group, Gulf of Carpentaria, Northern Territory

Anchorage 1 (14.xii): N of Three Hummock Point (15°38′S, 137°04′E), Vanderlin Island ('Island g' during the voyage).

Shore work: for less than an hour, near the point (15.xii, a.m., Brown with Flinders). The Florula for this and other places in the group of islands, mentioned by Brown in his Diary, has not been found.

Anchorage 2 (15.xii): S of Urquhart Islet (15°30′S, 136°57′E; ('Island h_2').

Shore work: on the islet (16.xii, a.m., Brown with Flinders).

Anchorage 3 (16, 22.xii): off Cabbage Tree Cove of North Island ('Island h') and in the channel between Red Bluff of that island and Observation Island ('Island h_3'; 15°37′S, 136°55′E).

Shore work: on North Island, about Red Bluff (16.xii, p.m.) — at Cabbage Tree Cove (17.xii, Good with Flinders) — on North Island a few hours, Brown a.m./walk on North Island to what seems vicinity of North Hill (15°33′S, 136°52′E), Good (18.xii) — [after return from anchorage 5] — an hour on Observation Island (22.xii, Brown) — walk across North Island to Macassar Bay (23.xii) — briefly (?) on North Island abreast of the ship (24.xii) — by yawl to Vanderlin Island and back, walk along shore of that island, probably about Denten Point (25.xii).

Anchorage 4 (19.xii): off (SW of) Wheatley Islet ('Island g_2'; 15°36′S, 136°59′E).

Shore work: in 'forenoon' on Wheatley Islet, then to W side Vanderlin Island for walk to Cape Vanderlin, 'Cape P' (19.xii, Brown with Flinders and others).

Anchorage 5 (20.xii): at E entrance to Centre Channel, between North and Centre islands, and N of the E point of Centre Island ('Island hh').

Shore work: about the S point of North Island (20.xii) — to Survey Bay (Centre Id), then to Craggy Islands and back through Centre Channel (21.xii, Good with Flinders) — [back to anchorage 3,22.xii].

31 December 1802–1 January 1803 Maria Island, Gulf of Carpentaria, Northern Territory ([Carpentaria] 'Island 1' during the voyage)

Anchorage (31.xii): off rocks at S side of Maria Island (14°54′S, 135°44′E).

Shore work: Good has 'ranged this island' but as he and Brown agree they were back on board before 9 a.m. the ranging must have been limited (1.i, a.m.). The 'Catalogue of Plants observd', mentioned in Brown's Diary, has not been found. Two of four rock samples taken are known.

4 January 1803 Malagayangu District, Arnhem Land, Northern Territory ('Mainland opposite Groote Eyland' in Brown's rock catalogue)

Anchorage (4.i): about 13°52′S, 136°01′E.

Shore work: walk 'Southerly' from landing place, 'nearly parallel to the beach', to a lake (13°53′S, 135°59′E) between which and the beach an aboriginal burial site found (4.i). Brown remarks in the Diary he counted 'upwards of 200' plants in this neighbourhood, 'about 26' of which 'we had not before seen'. The plant catalogue to which he refers is unlocated.

5–17 January 1803 Groote Eylandt and vicinity, Gulf of Carpentaria, Northern Territory

Anchorage 1 (14.i): *c*4km NNE of Chasm Island (13°40′S, 136°35′E).

Shore work: on Chasm Island and a 'low Island opposite' (14.i, Brown with Flinders, Bauer and Westall). Brown claims he alone went to the 'low Island', perhaps the islet SE of Chasm Island.

Anchorage 2 (14.i): in Northwest Bay, *c*1.5km of Finch Island (13°43′S, 136°34′E).

Shore work: vicinity of the bluff head of Groote Eylandt E of Finch Island and on the plain to SE (15.i) — on Winchelsea Island ('Island p') (16.i, Good with Bauer and Allen).

18 January 1803 Bustard Island, Gulf of Carpentaria, Northern Territory ('Island q_1')

Anchorage (18.i): about 13°44′S, 136°24′E, off S point of the island.

Shore work: on Bustard Island (18.i, Brown with Flinders, Bauer and Westall). A party of men seeking turtle stayed on shore overnight. The catalogue of plants referred to by Brown in the Diary has not been found. Burbidge (1956: 233) omits Bustard Island from her list of collecting localities. Low Sandy Islet ('Island q'), which she includes, was not in fact visited by the naturalists.

19 January–1 February 1803 Blue Mud Bay, Arnhem Land, Northern Territory

Anchorage 1 (19.i): *c*2km S of Burney Island (13°35′S, 136°14′E), 'Island r' during the voyage.

Shore work: on Burney Island 'about an hour & half' according to Brown (19.i, p.m.).

Anchorage 2 (20.i): *c*3km S of SE point of Morgans Island (13°28′S, 136°05′E), 'Island s'.

Shore work: 'remaind about an hour & half' (Brown) on Morgans Island (20.i, p.m.) — walk across Morgans Island and return before a skirmish with aborigines (21.i). The body of a presumed victim of the previous day's affray was dissected 22.i, no doubt by Bell and Brown, on board ship which early that afternoon sailed further into Blue Mud Bay.

Anchorage 3 (26.i): off (W of) the mainland point Cape Shield (13°20′S, 136°20′E), 'Point T' during the voyage.

Shore work: walk across Cape Shield peninsula to the gulf (E) side, then N to a fresh-water lake (13°18′S, 136°21′E) and return (26.i)

Anchorage 4 (27.i): about 13°15′S, 136°08′E, off the W shore of Point Blane peninsula, 'Point S' during the voyage.

Shore work: Brown and a sailor became disoriented during work on the peninsula, they had to sleep out and return next morning along shore round the point (27-28.i, Brown) — on Point Blane peninsula (28.i, Good and Allen). Although *Investigator* moved on next morning, adverse weather prevented her clearing Blue Mud Bay until 1.ii.

2–11 February 1803 Caledon Bay, Arnhem Land, Northern Territory ('Arnhem South Bay' of the log, 'Arnheim South Bay' of Brown)

Anchorage (3.ii): in Grays Bay, *c*3km NE of Middle Point (12°48′S, 136°33′E). Grays Bay is the name now given the N branch of Caledon Bay; it is separated from the Gulf of Carpentaria by a peninsula terminated to the S at Point Alexander ('Point U_2' of the log and supposed by Brown to be 'Cape Arnheim'). During the stay here Flinders had tents set up on the W shore of the peninsula, opposite his ship.

Shore work: on peninsula E of the ship a planned walk to sandhills *c*4km N of the landing place had to be abandoned, mangroves about Nanjiwoi Creek barred the way and aborigines walking with the party absconded with a hatchet and musket (4.ii, a.m.) — interview with aborigines at the tents from which Brown compiled lists of their names and words used for parts of the body and local plants, later in the day Brown took boat with Flinders and Westall to S shore of Caledon Bay/Good collected near the tents for his garden (5.ii) — Brown, Flinders and Westall set out early for the summit of Mount Caledon ('Point U_1'; 12°54′S, 136°31′E) and having climbed it returned to the ship/Good continued his work for the garden, staying near the tents (6.ii) — by boat to N shore of Grays Bay where work restricted by advancing aborigines and a skirmish (8.ii, Brown, Good, Westall and Allen) — by boat to Middle Point, there 2 hours (9.ii, a.m., Brown, Good and Allen) — briefly, on Dudly Island ('Island v_1'; 12°53′S, 136°44′E) as *Investigator* was leaving Caledon Bay (11.ii, a.m., Brown with Flinders and Bauer).

13–17 February 1803 Melville Bay, Arnhem Land, Northern Territory ('Arnhem North Bay' of the log, 'North Arnheim Bay' or 'Arnheim North Bay' of Brown)

Anchorage (13.ii): in Gove Harbour, *c*0.5km NW of Halftide Point.

Shore work: walk on N shore Gove Harbour (i.e. on Gove Peninsula), perhaps with Flinders to Dundas Point (13.ii, p.m.) — on island/peninsula forming E side of

Gove Harbour, walk from Halftide Point to Drimmie Hill (and probably Drimmie Head, 12°14′S, 136°42′E) and back, Brown and others/examination from boat of NE part of Gove Harbour (Inverell Bay), Drimmie Head peninsula and islands adjacent, Bauer with Flinders and Westall (14.ii) — N shore Gove Harbour, in evening (15.ii, p.m.) — by boat to Strath Island (*c*1km S of Drimmie Head) where pyrolusite and *Sonneratia alba* Sm., Sonneratiaceae, found (the latter 'seen for the first time by me'), then to point *c*3km E of Drimmie Head and back to ship, crossing at high tide the isthmus (now a causeway) joining Drimmie Head peninsula to the mainland (16.ii, Brown with Flinders and Bauer).

17–27 February 1803 The English Company's Islands, Northern Territory (Brown here followed the island notation of the log, prefacing localities on labels and in the rock catalogue with 'North Coast')

Anchorage 1 (17.ii): off S point of Cotton Island ('Island y_1'; 11°52′S, 136°28′E) and E of Pobassoo Island ('Island y_2'; 11°55′S, 136°27′E).

Shore work: E side Pobassoo Island, walk up gully to high ground and back to beach abreast of ship (18.ii) — on Pobassoo Island (19.ii, Good) — on Cotton Island, walk up valley draining SW part of island to hill at its head then back to beach opposite ship (20.ii) — on Pobassoo Island, 'crossd over to a valley I had not before seen', Brown/boat journey to NE point of Cotton Island, Bauer with Flinders and Westall (21.ii) — boat journey to Astell Island ('Island y_3'; 11°33′S, 136°25′E) (22.ii, Good with Flinders) — on Pobassoo Island to plant coconuts and potatoes (23.ii, a.m., Good). It may be added that discrepancies at this anchorage between Good's record and those of Flinders (1814) and Brown are generally resolved in favour of Good. His account agrees better with that of the ship's log.

Anchorage 2 (23.ii): off NE point of Inglis Island ('Island z'; 12°03′S, 136°12′E) and S of Bosanquet Island ('Island z_4'; 11°57′S, 136°20′E).

Shore work: on Inglis Island, at NE end, Brown and Good?/on Bosanquet Island or the small island between it and Inglis Island, Bauer (24.ii) — where Bauer had been the day before, in search of 'Guilandina Bonducella' (*Caesalpinia bonduc* (L.) Roxb., Leguminosae), Good a.m./and further search for the plant, in part successful, by Brown p.m. (25.ii) — on Bosanquet Island or its small neighbour (Good), though Brown claims it was Inglis Island (26.ii).

28 February–5 March 1803 Arnhem Bay, Arnhem Land, Northern Territory ('(North Coast) Bay No 3' of the log, and of Brown)

Anchorage 1 (28.ii): off S shore Mallison Island ('Island α'; 12°11′S, 136°08′E).

Shore work: on S side of Mallison Island (1.iii, a.m.).

Anchorage 2 (2.iii): off an island, then thought a peninsula ('Point Y_2'; 12°12′S, 136°19′E), at W side of entrance to Burungbirinung River.

Shore work: on the island 'Point Y_2', Good p.m., a scorbutic ulcer on Brown's left foot prevented him from landing with Good/Flinders, with Bauer and Bell, began a boat survey of Arnhem Bay, they spent this night on a patch of beach among mangroves near 12°18′S, 136°20′E (2.iii) — again on the island 'Point Y_2', Good and Allen a.m./boat party to Low Island (12°22′S, 136°10′E) and S shore of bay near 12°26′S, 136°09′E before returning to Low Island for the night (3.iii).

Anchorage 3 (4.iii): *c*3km of Everett Island ('Island α_1'; 12°15′S, 136°03′E).

Shore work: on Everett Island, Good and Allen p.m./boat party moved from Low Island to Hardy Island ('Island α_2'; 12°18′S, 136°03′E) and then to a mainland point ('Point Y_3'; 12°24′S, 136°01′E) before returning to ship at anchorage 3

(4.iii). Brown had been unable to work ashore since the visit 1.iii to Mallison Island; Flinders returned from the boat survey similarly afflicted. It was time to leave the coast and seek fresh provisions at the nearest likely source, Timor.

12 March 1803 New Year Island, Northern Territory

Anchorage (12.iii): off New Year Island (10°55′S, 133°02′E).

Shore work: 'walkd nearly round the Island' in less than 3 hours (12.iii, Good). Good accompanied a party sent to seek turtle. Brown did not land; the locality appears in his rock catalogue as 'New Years Island North Coast' with attribution to Good.

31 March–8 April 1803 At Kupang, Timor

17–21 May 1803 Goose Island Bay, Archipelago of the Recherche, Western Australia (Previously visited 14-17 January 1802)

Anchorage (17.v): *c*1km E of Goose Island and *c*2km NE of the anchorage 14.i.1802. Dysentery had spread in the ship since leaving Timor, where Flinders could obtain only fresh provisions. He hoped this place would supply him with geese for the sick, seals for lamp-oil and much-needed salt from the lake. The visit, marred by the first fatality from dysentery among the crew, was a disappointment.

Shore work: Brown and Good's records end 17.v, Good's for ever. Good had succumbed to dysentery and was incapable of work on shore. Scorbutic sores again affected the commander's mobility, as they had at Arnhem Bay over two months earlier. His record of the second visit to Goose Island Bay has nothing about Brown and his people. Yet something was done. There is, for instance, a specimen of *Gyrostemon ramulosum* Desf., Gyrostemonaceae, in the BM(NH) herbarium (Bennett 3044B) which was collected on Middle Island at this time. That Bauer botanical painting 123 (BM(NH) Botany Library) appears to relate to this sample suggests the artist was among those still able to work.

9 June–28 November 1803 Port Jackson/Sydney, New South Wales

Investigator came to anchor in Sydney Cove about noon 9.vi.1803. The days and weeks following were to see Brown's circumstances profoundly changed. He kept no Diary as a town-based naturalist, and without the careful recording of a Peter Good or the regularity of a ship's log it becomes a difficult business to follow Brown's activities. *The Sydney Gazette and New South Wales Advertiser*, begun 5 March 1803, is of help, so too are letters but most of the detail must come from labels to Bauer's paintings and, especially, from original slips with specimens in the BM(NH) herbarium. An incomplete index to dated and located items in the Brownian collection exists in the BM(NH) Botany Library but that has had to be supplemented by much extra searching in the herbarium by my colleagues in London. Most of Brown's labels bear at least a general locality, many also a date (some a day but more commonly just a month and year). Yet those labels must ever be interpreted with great care. Brown was not always careful with time and in places mistook direction. He also annexed, without acknowledgment, other collectors' material on occasion. The finding of a dated and localized label, assuming the detail is correct, brings no certain evidence that Brown (or Bauer) was at the place at the time. A digressionary example will illustrate.

Groves and Moore (1989: 86) refer, as their no 185 (Bennett 66), to an herbarium sheet for the fern *Adiantum hispidulum* Sw., supposedly gathered by Robert Brown in Australia. Three old labels accompany the sheet, one indicating 'Port Jackson with no date, the second 'North rocks 8 August 1802' and the third 'Dove Dale Feb 1804'. The first, of course, might be due to Brown but the lack of a date is no help. As to the other two, although Brown had visited North

Rocks 18.vi.1802 he was at Port Curtis with Flinders 8.viii.1802 and at the time of the Dove Dale collection he was at the Derwent or on his way there. Bauer certainly was somewhere about Sydney in February 1804 but the Dove Dale locality (now Bents Basin on the Nepean River) was a Caley collecting place. Indeed it is known Caley was there 18-19.ii.1804 (Caley, 1966: 104). Surely he would have recorded the fact if Bauer had gone with him, or had been there independently at the time. It seems likely to me the North Rocks and Dove Dale records are annexed from Caley. And that is the sort of problem one must keep in mind when following Brown by herbarium labels.

Activity: Peter Good died 12.vi and was buried in Sydney 13.vi — *Investigator* was officially condemned 14.vi — Flinders received the offer of *Porpoise* with a tender to complete his survey, the offer subject to inspection when *Porpoise* returned from a voyage now pending (16.vi) — *Porpoise* left for Tasmania, with Caley a passenger (17.vi) — *Porpoise* returned, driven back by storms (3.vii) — having decided she would not suit his survey, Flinders sought and was offered *Porpoise* to return to London there to seek a replacement for *Investigator*, he accepted the offer (11.vii) — Brown, Bauer and Allen now applied to stay in the colony for a time (13.vii) — permission was granted for them to stay until the return of Flinders or for 18 months from the day of his departure, whichever was the shorter (17.vii) — accordingly Flinders left provisions for them for the stated period and the governor gave them the use of a house in Sydney; the arrangements appear to have been completed before Brown wrote to Banks and to Charles Greville (6.viii) — *Porpoise* sailed for England, with Allen a passenger (10.viii) — evidence of collecting begins next day and continues at various localities about Sydney and between Sydney and Botany Bay (11-21.viii) — Sydney and Parramatta (21-24.viii) — an orchid, Sydney (27.viii, Bauer) — Sydney, South Head and between (28-31.viii) — Sydney and between Sydney and Botany Bay (1-8.ix) — various specimens from the Hawkesbury, Richmond Hill etc indicate an excursion (8-24.ix), perhaps by Bauer but not Brown who was in Sydney when Flinders returned (8.ix) with news of the *Porpoise* shipwreck and when he sailed again (20.ix) with the relief ships, further, Brown wrote to Banks and Greville again (16.ix) and that day collected at Bennelong Point — an orchid, Bauer (25.ix) could be a sign of return to Sydney — between 'Port Jackson' and South Head (26.ix) — between Sydney and Georges River, there, and between Georges River and Sydney (28.ix-4.x) — orchids, Georges River (29.ix, 4.x) point to Bauer and a collection Parramatta (4.x) might be Brown apart, or Caley — Sydney and South Head (5-8.x) — near Sydney (11.x) — Parramatta, North Brush, Brush Farm (11-12.x) — Sydney (13-14.x) — between Sydney and Botany Bay (16.x) — Prospect Hill, Cowpastures, Mt Hunter (18?-24.x, probably Brown with Caley though Caley (1966: 228) has visit with Brown 'November') — Cooks River (20.x) implies Bauer apart — Parramatta (24.x) might be Brown returning from the Cowpastures, Port Jackson (24.x) seems more likely Bauer — *Resource* returned from Wreck Reef (27.x), *Francis* with seeds salvaged from the wrecked *Porpoise* came in (30.x) — collecting at Brickfields, Sydney (28.x) — Cooks River, Botany Bay etc (29.x-1.xi) and Sydney to Parramatta, Nepean and Grose Rivers coincide exactly in time, implying separate activity — likewise Sydney and South Head (2-5.xi) overlaps Parramatta, Lane Cove, Hawkesbury, Richmond Hill, Nepean and Grose Rivers and Badgery's Farm (4-21.xi) but as Bauer painting 172 depicts an orchid from 'the banks of the lake on the way from Sydney to Botany Bay Nov 12 1803' it seems more likely Brown went to the Hawkesbury this time — between Port Jackson and Botany Bay and

between Sydney and South Head dated the same day likewise suggest separate activity (23.xi) — news reached Sydney 24.xi of the arrival at Port Phillip of David Collins [1756-1810] with people to form a settlement there, the governor, P. G. King [1758-1808], then decided to send despatches to Collins by *Lady Nelson* and permitted Brown to accompany her — *Lady Nelson* sailed for Port Phillip 28.xi, with Brown a passenger and no doubt expecting no more than a brief visit to a place seen iv-v.1802. Bauer remained in Sydney. Brown resumed his Diary 28.xi.1803 but dated it 1804, a lapse which has misled many, among them Mabberley (1985: 121).

12–31 December 1803 Kent Group, Bass Strait, Tasmania ('Kent's Group' or 'Kent's Islands' of Brown) *Lady Nelson*, bound for Port Phillip, had been forced to seek shelter there from gales.

Anchorages (12, 27.xii, and others between from which it is not known when, or even if, there were landings): in East Cove of Deal Island (32°29′S, 147°21′E).

Shore work: Brown's plant labels, variously inscribed 'Decr 12-19 1803' and 'Decr 12-19 1804', suggest an early start but it seems unlikely he landed 12.xii as the ship came in late — 'walked over a considerable part of the Eastern Island' (i.e. Deal Id) on 13.xii and 14.xii, a.m. — attempts to get clear of the islands (14, 15, 20, 24.xii) failed, each time *Lady Nelson* being forced back to East Cove where she was storm-bound 17, 18, 19, 23.xii and from 27.xii — on 28.xii *Francis*, seeking shelter on a run from Port Phillip to Port Dalrymple, joined *Lady Nelson* in East Cove — *Francis* being in a 'crazy' condition it was resolved her mission to seek an alternative site for the people at Port Phillip to settle be transferred to *Lady Nelson* — His Majesty's mineralogist A. W. H. Humphrey, with others, thus came to join Brown as passengers on *Lady Nelson* and begin an occasional association with Brown in the field — Humphrey and Brown apparently worked together 29-30.xii, in that time climbing Flag Hill behind East Cove; both collected rocks and minerals (now lost). In notes headed 'Mineralogy' (Vallance and Moore, 1982: 32) Brown refers to rocks of 'Both Islands', which suggests a visit to Erith or Dover Island, facing East Cove. *Francis* left 30.xii for Port Jackson with letters from Brown, that to Banks is known. *Lady Nelson*, with Brown and her new passengers, departed 31.xii for Port Dalrymple.

1–19 January 1804 Port Dalrymple and River Tamar, Tasmania ('Port Dalrymple, Van Diemens Land' of Brown)

Anchorage 1 (1.i): about 41°04′S, 146°48′E, off Lagoon Beach, on E side of entrance to Port Dalrymple.

Shore work: according to Humphrey, Brown 'stopped in a Valley attracted by some Plants' while he and their companions walked on towards Outer (now York) Cove (41°07′S, 146°49′E) (1.i) — Brown walked to Low Head (41°03′S, 146°47′E) and then to York Cove and back (2.i).

Anchorage 2 (3.i): in York Cove.

Shore work: 'walkd a little into the country' about 2 hours, from York Cove, Brown (3.i) — 'walkd to the nearest hills' (probably The Buffalo, 41°05′S, 146°50′E), again met aborigines, as some had 1.i (4.i) — walked up creek draining from NE into York Cove (5.i, a.m.).

Anchorage 3 (5.i): off Inspection Head (41°09′S, 146°49′E), at the entrance to West Arm ('Western Arm' of Brown) of Port Dalrymple.

Shore work: 'walkd about half a mile into the country', Brown (5.i, p.m.) — probably by boat to head of West Arm then walk W to Flowers Hill (41°10′S, 146°42′E) and back (6.i).

Anchorage 4 (7.i): '¾ mile above Middle Island' (41°09′S, 146°52′E).
Shore work: landed.
Anchorage 5 (7.i): off Egg Island (41°14′S, 146°58′E).
Shore work: landed.
Anchorage 6 (7.i): off Nelsons Shoal (41°20′S, 147°02′E).
Shore work: in evening landed and walked a little way up a creek, perhaps Muddy Creek on W side of the river (7.i, p.m.) — by boat in search of water, landed and dug without success (8.i, a.m.)
Anchorage 7 (8.i): above Upper (now Tamar) Island, near 'where the river becomes narrower' (the river was named the Tamar later in 1804).
Shore work: Brown stayed on board but two others went up river by boat, discovering the junction of North and South Esk rivers and, importantly for them, fresh water (9.i) — Brown and Humphrey visited the river junction (site of present Launceston) and entered the gorge of South Esk River (Cataract Gorge) (10.i).
Anchorage 8 (11.i): near anchorage 6 (Humphrey called the place Shoal Bay).
Shore work: landed in evening, Brown (11.i, p.m.) — a wooding party landed (12.i, a.m.).
Anchorage 9 (12.i): near anchorage 5.
Shore work: Brown landed 'for a few minutes' in the evening (12.i, p.m.) — landed at mouth of Supply River, water casks filled while Brown took a short walk on its banks and Humphrey carved his initials on an outcrop of dolerite (13.i).
Anchorage 10 (14.i): near anchorage 4.
Shore work: 'walkd over part of the flat country behind Middle Island', that is the country behind Bell Bay, Brown (14.i, p.m.).
Anchorage 11 (15.i): 'between Green Island & Middle rock', at the mouth of York Cove; later, nearer anchorage 2.
Shore work: Brown and others sought to interview aborigines on E shore but they retreated when the boat approached, a landing on Middle Rock on the way back to the ship (15.i).
Anchorage 12 (18.i): near anchorage 1.
Activity: neither Brown nor Humphrey appears to have landed after 15.i but William Collins [1760?-1819] completed his survey, visiting the opposite shore. *Lady Nelson* sailed for Port Phillip early 19.i.

21–30 January 1804 Port Phillip, Victoria
Anchorage (21.i): in Sullivan Cove, off present Sorrento where David Collins had set up his camp.
Shore work: Brown had been here before (26.iv-3.v.1802) and left few notes of this visit — according to Humphrey, he and Brown went to Arthurs Seat, camping at its foot (24-25.i). *Lady Nelson*, with Brown still a passenger, sailed 30.i for the River Derwent, Tasmania, where Collins had decided to shift his settlement. Humphrey left the same day on *Ocean* for the same destination.

9 February–9 August 1804 River Derwent, Tasmania ('River Derwent, Van Diemens Land' of Brown)
Anchorages (*Lady Nelson*, 9.ii; *Ocean* 15.ii): Risdon Cove (42°49′S, 147°19′E). In what turned out to be a protracted stay, Brown lived on *Lady Nelson*, first at Risdon Cove and then at Sullivan Cove (Hobart) until near the end of the month when the vessel was being prepared for departure for Sydney. Brown plainly had found sufficient of interest and was not tempted to leave yet. He therefore moved on board *Ocean* at Sullivan Cove until she had to leave for Port Phillip (24.iii). Brown then left Sullivan Cove for a house at Risdon and this served for the remainder of his time at the Derwent.

Activity: collecting at Risdon Cove (11.i) — and at Herdsmans Cove (12.i) — ascent of Table Mountain (now Mt Wellington), the first night spent 'a little below the summit' (18-20?.ii, Brown but not Humphrey) — ascent of Mount Wellington (27-28?.ii, Brown) — collecting 'Derwent River' (29.ii) — Brown, Humphrey, chaplain Knopwood and John Mertho (in command of *Ocean*), joined at Risdon by surgeon Jacob Mountgarrett [1773?-1828], set out 5.iii on a boat journey up the Derwent, the first night spent about Granton, on 6.iii they reached the rapids near Lawitta (3km above New Norfolk), Humphrey and Mountgarrett then turned back but Brown and others stayed this and the next night, according to Knopwood on 7.iii Brown 'went up the mountains a-botanizing' while he and Mertho went 'a-shooting', they struck camp in bad weather 8.iii and returned to Sullivan Cove (5-8.iii) — Brown and Mertho had an interview with aborigines at Sullivan Cove (9.iii) — this time with Humphrey, Brown went to Mount Wellington, probably a late start, the night 12.iii spent in a hollow tree 'at the Foot of the Mount', then to the summit and back to the tree 13.iii, to the summit again and descent to the tree 14.iii, and return 15.iii to Sullivan Cove (12-15.iii) — on 27.iii Brown, Humphrey and Mountgarrett set out by boat from Risdon 'with 10 days provisions, to go to the head of the river' (Knopwood), reached the first rapid (cf 6.iii) that night and camped there, next day on foot to about present Clarendon, to the junction with the River Ouse by night 29.iii, then along Derwent to about junction with Black Bobs Rivulet by night 30.iii, next day the party seems to have left the Derwent and struck into country between the Nive and the River Dee (nearer the latter if Brown's directions are reliable), the return began 1.iv and by 4.iv they had reached the first rapid and by 5.iv were at Risdon (27.iii-5.iv) — Brown, Knopwood and Mountgarrett by boat from Risdon to Sullivan Cove and back (7-8?.iv) — on 20.iv, according to Knopwood, Brown returned to Sullivan Cove from a journey by which he had tried 'to get to the river Ewen [Huon], but could not', Brown himself left no record of this but where he went can be surmised, after crossing the summit of Mount Wellington he must have followed the stream (North West Bay River) which appears to drain towards the Huon but in fact turns back in a deep gorge off the mountain, once in the gorge Brown presumably had to follow where it led and arriving at North West Bay walked back (N) to the settlement (?-20.iv) — Brown tried again, setting out 2.v with Humphrey to spend the night again at the hollow tree (cf 12.iii), next day over Mount Wellington to camp just below the head of North West Bay River, on 4.v they avoided Brown's earlier mistake by leaving the river to cross the W ridge of the summit but spent an uncomfortable night on N slope of Mount Montagu, next day (5.v) down Montagu Creek to Mountain River which was followed to the Huon (7.v) and a night's camp about present Huonville, next day down the E side of the Huon to about Cradoc (43°07′S, 147°02′E) where a night's camp, next day went back upstream past the campsite 7.v to spend night 9.v about Ranelagh, then further upstream on 10.v to their limit about Glen Huon, after spending the night there they returned to the campsite near Cradoc from where, on 12.v, they crossed into the valley of Kellaways Creek (also Sandfly Rivulet) and followed it to about Pelverata, on 13.v Brown and Humphrey went over Herringback (43°00′S, 147°08′E) to the head of either Cooke or Allen Rivulet, next day the rivulet (Brown's record leaves doubt as to which it was) was followed down and on 15.v they found it joined the North West Bay River and thus led to the bay, on 16.v Brown and Humphrey walked back from North West Bay to Sullivan Cove to end an extraordinary piece of early exploration in Tasmania (2-16.v) — Knopwood records Brown and

Mountgarrett went with him by boat from Risdon to 'Hobart Town Camp' (23.v) — Brown's next recorded journey was an attempt to cross the N part of the Mount Wellington summit area to Collins Bonnet and Trestle Mountain, he set out from Risdon 28.v with his servant (J. W. Porter) and some assistants crossing by boat to Prince of Wales Bay then walking up Humphrey Rivulet onto the mountain, next day as the climb continued Porter became ill and Brown left him with an assistant while he botanized, but on 30.v Porter was too ill to go on so Brown and the others brought him down to the river where fortunately a boat was passing, having seen Porter safely off Brown headed S for 'settlers rivulet' (New Town Rivulet) where he camped 30.v, next day he ascended Mount Wellington (probably by his 'usual' route from Sullivan Cove) but on reaching the summit he injured his foot, managing to get clear of the summit he spent an uncomfortable night (31.v) in 'a hut of boughs', Brown's record of the journey ends with him 1.vi barely able to stand, it is not known when he got down (28.v-?.vi) — by 12.vi, however, he was out again, on a boat journey from Risdon with John Bowen [1780-1827] and Mountgarrett down the Derwent to D'Entrecasteaux Channel, the first night spent at 'McCluers' (now Barnes) Bay, North Bruny Island, a storm 13.vi restricted them to the bay and not until 15.vi did they manage to escape and move to Isthmus Bay, next day it was on to 'Henrietta Creek' (probably Garden Island Creek) not far inside the mouth of the Huon River, from there the party moved to Port Esperance ('Port de l Esperance' of Brown) on 17.vi and next day one of the streams there (probably the Esperance River) was examined for an unstated distance by boat and on foot, the travellers returned to Risdon 20.vi at sunset (12-20.vi). Brown's Diary record of activity in Tasmania ends with that return. How he spent the 7 weeks until he sailed 9.viii on *Ocean* for Port Jackson is largely unknown. Knopwood saw him a few times more but he also mentions bad weather on nearly the half the days of July. Further, the ill-health which troubled Brown back in Sydney may well have begun at the Derwent. That and the weather could have kept him inside at Risdon compiling the Florula Montis Tabularis which forms part of the Diary.

24 August–11 October 1804 Port Jackson and Sydney, New South Wales

Anchorage (*Ocean* 24.viii): in Sydney Cove. It is presumed Brown returned to the house in Sydney provided for him and Bauer by Governor King before Flinders left in 1803.

Activity: Brown arrived to find Bauer had just sailed (21.viii) for Norfolk Island (and would not return until 11.iii.1805) — he had thus to continue working on his own, but from Sydney Caley was accessible and the few Diary entries made at this time refer to Caley, and Brown's ill-health — there is no evidence of collecting or other activity until 14.ix when Brown went to visit Caley — 'Walkd from Sydney to Parramatta' (14.ix) and there inspected Caley's collection, the subject of extensive notes in the Diary, on 15.ix walked and collected at Parramatta but most of the day spent with Caley, his orchids and material from the Hunter River — walked back to Sydney 16.ix, botanizing on the way — described plants (17.ix) but then Brown admits trouble: 'Indisposd loss of appetite, incapable of describing or observing' (18-20.ix) — despite this he managed to finish arranging his Tasmanian collection 'ready for packing' and on 19.ix showed it to Caley and William Paterson [1755-1810], lieutenant-governor and amateur botanist, who had called on him — more plant descriptions are dated 21.ix but there is no further sign of activity (apart, perhaps, from an undated plant list) until 9.x when he was preparing to sail by the colonial vessel *Resource* for the Hunter River. At the Derwent Brown had complained his access to boats depended on

chance. To avoid that difficulty at the Hunter (though Brown does not mention it) Governor King lent him a boat and this was taken with Brown when *Resource* sailed 11.x.

12 October–?18 November 1804 Hunter River, New South Wales ('Coal River' or 'Hunter's River' of Brown)

Anchorage (12.x): in the Hunter River, at Newcastle ('King's Town', 'Kingstown' or 'Kingston' of Brown).

Activity: a short walk about the town and visit to the coal mine, in the afternoon a walk towards 'Mangrove Creek' (part of Throsby Creek drainage) (13.x) — by boat 14.x with Charles Menzies [1783-1866], the commandant, to 'Ash Island' (later Moscheto Island but since destroyed by 'reclamation'), on the way back landed at 'Chapman's Island' (now lost to industry at Carrington) — walked in the neighbourhood of 'Kingston' (15.x) — left by boat 16.x to go up river, camped that night *c*3km below present Raymond Terrace — continued up river and 'stopt for the night about a mile below the junction of Paterson's & William's Rivers' (in fact, respectively the Hunter and Paterson rivers) — on 18.x Brown continued up the Hunter (his Paterson) to between present Morpeth and Maitland, the course of the river then being far more winding than it is today — on up river to 'about two miles above mount Anna' (Comerfords Hill, 32°41′S, 151°34′E) and there slept (19.x) — up river to the base of 'Mount Elizabeth' (Mount Hudson, 32°38′S, 151°27′E), climbed it and spent the night nearby (20.x) — began return down river 21.x, spent night as on 18.x — returned to the settlement 23.x — in neighbourhood of 'Kingstown' (23-28.x) but 28.x again left in the boat with intention to 'examine the banks of Hunter's River' (modern Williams River) and this night camped as on 16.x — on up Williams River (Brown's 'Hunter's River') to just below present Clarence Town (29.x) — on 30.x Brown reached the navigable limit of the river and went only a short way further, probably not much beyond the junction with Boatfall Creek (about 32°34′S, 151°48′E), he had a visit from aborigines this evening — next day when preparing to return the aborigines again appeared and attempted to steal muskets, Brown and his servant received blows and one native was shot, perhaps fatally, the boat party retreated and spent night *c*4km below Clarence Town (31.x) — the next night was spent by the (present) Williams River 'about a mile & half above the commence[ment] of the cedar arm' (which Brown also knew as the 'Paterson's River' but is now the Hunter) — on 2.xi Brown's boat party followed the present Hunter to the junction with the modern Paterson River (his 'William's' or 'Williams') and then the latter to end the day between present Woodville and Paterson — continued up modern Paterson River to about townsite of Paterson (3.xi) — on 4.xi the party reached beyond Gostwyck (32°34′S, 151°36′E) and climbed 'a high round hill' (Mount Johnstone), with a description of the view Brown's Australian Diary ends. It is unclear when Brown returned to Newcastle; a plant labelled 'Hunter's River' and dated 7.xi suggests he was then still out. The first date on a sample from 'Kingstown' is 10.xi, so he was back by then. 'Ash Island' on 13.xi and 'near Kingstown' 16.xi complete the record. A collection 'vicinity of Sydney' on 28.xi fixes return to Sydney and the only arrival from Hunter River in the period was the colonial vessel *Bee* which came in 20.xi. It had to be Brown's conveyance.

20 November 1804–23 May 1805 Sydney, New South Wales

With his return from the Hunter River Brown's travels in Australia were virtually at an end. Thereafter he would only make occasional forays from Sydney in search of specimens, the longest being another visit to the Hawkesbury, roughly

24.xii-2.i. He or Caley might have contributed material from Middle Harbour dated 23.ii. By the time Brown and Bauer were reunited (11.iii) trouble lay ahead. Governor King was becoming increasingly caught up in what seemed a case of piracy which had spread into his jurisdiction. King grew anxious to refer the matter to London and as message-carrier his attention fell on *Investigator*, once a hulk but since cut-down and tested on a run to Norfolk Island and back (with Bauer). Brown's last months in Sydney were much occupied in debate with the governor who plainly wanted to see Brown, Bauer and their collections leave with the papers he was sending to London. In the end, Brown was totally outmanoeuvred. The governor had sweet answers to all Brown's protests about the likely risk to the collections at sea in a vessel he knew from experience to be leaky. But the original slip with Bennett 4597 in the BM(NH) herbarium, *Baeckea brevifolia* (Rudge) D. C., Myrtaceae, indicating collection 5.v.1805 between Sydney and South Head, shows there was still enthusiasm amidst the anxiety. It is not hard to guess, however, that anxiety was uppermost just over a fortnight later, on 23.v.1805, when Brown and Bauer saw Sydney and Port Jackson disappearing into the distance for the last time. They must have thought it was a pretty awful way to go. *The Sydney Gazette* noticed their departure, opining their collections 'will be very acceptable to the Amateurs of Natural History'. We rejoice there was more to them than that. But at least the *Gazette* did not hope those of the Northern Lands would simply be entertained.

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A Review of Species Previously Identified as *Craterocephalus eyresii* (Pisces: Atherinidae)

L. E. L. M. CROWLEY and W. IVANTSOFF

(Communicated by P. M. SELKIRK)

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Recent electrophoretic and osteological work has shown that geographically widely separated populations of fish, all previously identified as *Craterocephalus eyresii*, are attributable to four distinct species. These are *C. eyresii* (Steindachner, 1884), *C. fluviatilis* McCulloch, 1913, and two new species, *C. centralis* and *C. amniculus*. Osteological differences between the first three species are minor, whilst the maxilla and premaxilla of *C. amniculus* are distinctly different. Electrophoretic studies indicate only a single fixed gene difference between *C. amniculus* and *C. fluviatilis* but the other three species differ considerably at a number of loci. There are three fixed gene differences between *C. eyresii* and *C. centralis* and at least seven between all other pairs. Morphologically, *C. eyresii*, *C. fluviatilis* and *C. centralis* are very similar. *C. amniculus* is distinguished from the other three by having a greater number of midlateral and transverse scales.

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INTRODUCTION

In separate studies in 1978, both Ivantsoff and Patten recognized and reviewed 10 species of hardyheads in the genus *Craterocephalus*. With recent work and more comprehensive collecting the number has now risen to 24 (see Ivantsoff *et al.*, 1987a, b; Crowley and Ivantsoff, 1988). Populations of hardyheads with a broad but disjunct distribution (central and South Australia, through the Murray-Darling Drainage System in New South Wales and in the Hunter River Region of central eastern New South Wales) were recognized as *C. eyresii*, (Ivantsoff, 1978, Patten, 1978) or as *C. fluviatilis* (McCulloch, 1913- see Ivantsoff *et al.*, 1987a). Some slight morphological variations between these populations were apparent, but were accepted as population variability in a single, widespread species.

In 1884, Steindachner described the atherinid species *Atherinichthys eyresii (= Craterocephalus eyresii)* but failed to designate type material or to give a particular type locality. McCulloch and Waite (1918) carefully examined specimens obtained from Coward and Strangways Springs in South Australia and identified them as indistinct from those described by Steindachner. They also pointed out that the Lake Eyre hardyhead was closely allied to *Craterocephalus fluviatilis* (McCulloch, 1913). Jordan and Hubbs (1919), in their review of atherinids, suggested Coward and Strangways Springs as the type locality basing their interpretation on a statement 'wärhend der Lake Eyre-Expedition gesammelt'.

Re-examination by Ivantsoff (1978) of McCulloch's type material, on which the original description of *C. fluviatilis* is based, showed that the holotype and two paratypes were distinct from the other paratypes; the former were identified at that time as *C. eyresii*, but recent work has shown this identification to be incorrect. The three other paratypes, one of which was figured, are now recognized as *C. stercusmuscarum fulvus* (see Ivantsoff, 1978; Ivantsoff *et al.*, 1987a).

In his study of variability in populations, Ivantsoff (1978) noted that midlateral and transverse scale counts in hardyheads from the Peel and Namoi Rivers were much

higher than those from southern reaches of the Murray-Darling River system, South Australian waters and the type locality.

The objectives of this study were: to examine morphological, osteological and genetic variation in populations identified as *C. eyresii*; to re-assess the relationships between the populations from the Finke River and Lake Eyre Drainage on the western side of the Flinders and Barrier Ranges and from the Murray-Darling Drainage to the east of those ranges.

Materials and Methods

Procedures used for measurements and counts are as reported in Crowley and Ivantsoff (1988); values were taken from thirty specimens of each species wherever possible. Alizarin stained specimens — following the method of Taylor (1967) — were used for osteology with three or more specimens of each species examined.

Electrophoresis was carried out following the methods of Richardson *et al.*, (1986). Fixed gene differences as suggested by those authors were used to indicate genetic relationships between populations. Ten specimens of each species were examined at twenty-one loci (see Table 1 for enzymes assayed).

Specimens designated as holotypes and paratypes are now deposited in The Australian Museum, Sydney (AMS); Northern Territory Museum of Arts & Sciences (NTM); University of Michigan Museum of Zoology, Ann Arbor Michigan (UMMZ); American Museum of Natural History, New York (AMNH); Western Australian Museum, Perth (WAM). Additional material from the following institutions has also been examined: Museum of Victoria, Melbourne (NMV); South Australian Museum, Adelaide (SAM), Macquarie University, (MQU).

Systematic Descriptions

Craterocephalus amniculus sp. nov.
(Fig. 1)

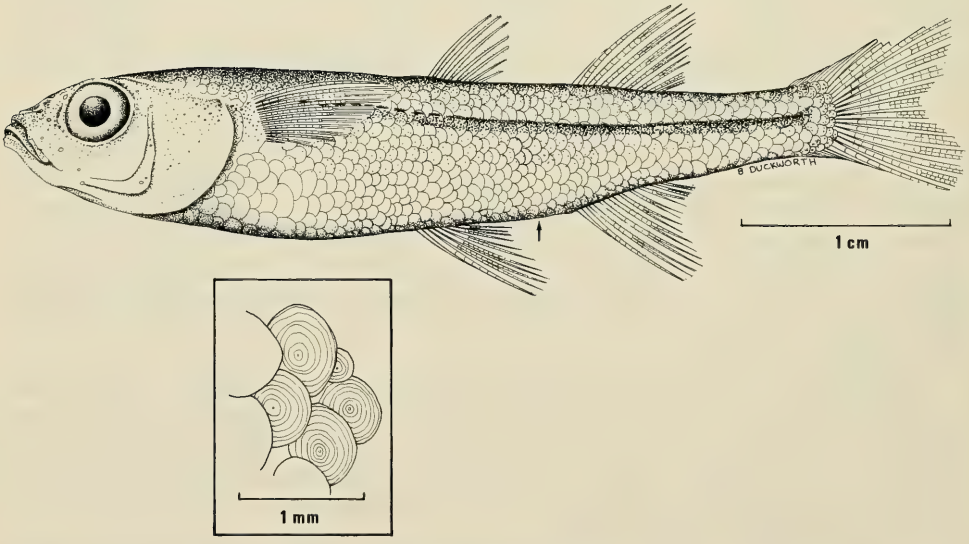

Fig. 1. Holotype of *Craterocephalus amniculus*, AMS I.28880-001, 40.0mm SL. Arrow indicates position of anus.

Craterocephalus eyresii: Lake, 1978:41 (in part); Ivantsoff 1978:245 (in part), 1980:133 (in part); Llewellyn, 1983:13 (in part); Merrick and Schmida, 1984:145 (in part).

Holotype: AMS I.28880-001. 40.0mm standard length (SL), collected with 2.5m seine, in shallow water over gravel, in Cockburn River, Nemingha, N.S.W. 31°07′S, 150°59′E. Collected by A. L. Crowley and L. E. L. M. Crowley, 13 February, 1987. For morphometrics and meristics of the holotype, see Table 2.

Paratypes: (21), AMS I.28880-002 (10, 25.8-44.2mm SL); WAM P.29891.001 (4, 32.0-40.6mm SL); NTM S.12526-001 (3, 36.6-45.5mm SL); UMMZ 214855 (2, 36.7-43.4mm SL); AMNH 58688 (2, 42.7-43.4mm SL). Locality and collectors for all paratypes as for the holotype.

TABLE 1

Enzymes assayed, number of loci scored, buffer and staining-system used following the methods of Richardson et al., *(1986)*

Enzyme Name and abbreviation	E.C. Number	Loci scored	Buffer
Adenosine deaminase ADA	3.5.4.4	1	B
Alcohol dehydrogenase ADH	1.1.1.1	1	B
Adenylate kinase AK	2.7.4.3	1	B
Aldolase ALD	4.1.2.13	1	D
Creatine kinase CK	2.7.3.2	1	D
Fructose-1,6-diphosphatase FDP	3.1.3.11	1	B
Fumarate hydratase FUM	4.2.1.2	1	B
Glyceraldehyde-3-phosphate dehydrogenase GAPD	1.2.1.12	1	D
Glucose dehydrogenase GLDH	1.1.1.47	1	B
Aspartate aminotransferase GOT	2.6.1.1	2	B
Glycerol-3-phosphate dehydrogenase αGPDH	1.1.1.8	1	B
Glucose-phosphate-isomerase GPI	5.3.1.9	2	B
Isocitrate dehydrogenase IDH	1.1.1.42	1	A
Lactate dehydrogenase LDH	1.1.1.27	1	B
Malate dehydrogenase MDH	1.1.1.37	2	A
Malic enzyme ME	1.1.1.40	2	B
Mannose phosphate isomerase MPI	5.3.1.8	1	B
Phosphoglucomutase PGM	2.7.5.1	1	B
Xanthine oxidase XO	1.2.3.2	1	D

Additional Material Examined: (included in counts and measurements) (Table 2): MQU I.77-3 (1, 31.8mm SL), Peel River, at Tamworth, N.S.W., 31°04′S, 150°53′E; MQU I-086 (5, 30.7-33.0mm SL) Glennies Creek, N.S.W., 32°33′S, 148°29′E; MQU I-001 (1, 40.7mm SL) Bowmans Creek, N.S.W., 32°25′S, 151°03′E. Material examined for osteology: AMS IA.333 (2), Warialda Creek, N.S.W., 29°36′S, 150°50′E; MQU IA.90 (1), Peel River, Tamworth, N.S.W., 31°04′S, 150°53′E; MQU IA.70-52 (2), Peel River, Tamworth, N.S.W. 31°04′S, 150°53′E.

Diagnosis: A species of the atherinid genus *Craterocephalus*, superficially appearing to be most closely allied to *C. eyresii* but differing from that species in the following: midlateral scale counts, 40.6 (37-48); transverse scale counts 15.9 (14-18). For a comparison of morphometric and meristic values of *C. amniculus, C. centralis, C. eyresii* and *C. fluviatilis* see Tables 2, 4, 5, 6. Differing osteologically from *C. eyresii*: in shape of maxilla; in ratio of symphysial part of dorsal process to total length of dorsal process of premaxilla; in shape of nasal bone; in medial process of pelvic girdle (see Fig. 2). Exhibiting fixed gene differences at 8 loci (see Table 3), when compared with *C. eyresii*.

Differing from all other species of the genus *Craterocephalus* by the combination of the following: midlateral 40.6 (37-48); transverse scale counts 15.9 (14-18); gill raker count 10.2 (9-11); shape of anterior medial process of maxilla. Scales of head and body smaller than in any other *Craterocephalus* species; scales with obvious circuli (see Fig. 1).

Description: Small, moderately robust fish, maximum known size 44.2mm SL. Mouth protractile, lips thin. Gape restricted by labial ligament, one third of way along mouth. Teeth few, moderately long and pointed, restricted to anterior part of both jaws. Other bones edentulous. Premaxilla short and not reaching vertical through anterior edge of orbit; dorsal premaxillary process reaching into interorbital space. Gill rakers moderately short, less than half diameter of pupil, first four often tuberculate. Scales small, almost circular, thin, but with circuli complete and obvious, appearing barely to overlap. Scales usually absent from dorsum of head, or if present, well spaced, small and circular. Opercles naked.

Colour: Live specimens (from Nemingha) dusky gold above dark silvery midlateral stripe and silvery gold below. Abdomen, chin, opercles and eyes, silvery. Dorsum of head, snout and lower jaw very dark. Caudal fin golden, dorsal fins dusky gold. Anal fin pale gold; ventral fins clear. Fish from other areas (e.g. Boiling Down Creek) paler than Nemingha specimens but similar in other features. Preserved specimens — cream to light brown, depending on length of preservation. Eyes dark. Upper half of body brownish and heavily peppered with melanophores. Lower half peppered lightly with melanophores, except for abdomen. Upper and lower body scales never outlined to form reticulate pattern. Dark peritoneum visible through body wall from origin of ventral fins to anus. Opercles, snout, premaxilla, maxilla and lower lip, speckled; dorsum of head very dark. Pectoral, first and second dorsal, anal and caudal fins with melanophores forming contours along spines and rays. Ventral fins clear.

Etymology: *amniculus* — meaning a small creek or stream, referring to the habitat where these fish are often found.

Distribution: *C. amniculus* has been collected in the Macintyre River, Warialda Creek, Peel and Cockburn Rivers, the Namoi River, and Boiling Down Creek which are all tributaries of the upper Darling River. Some specimens have also been collected from Glennies Creek and Bowmans Creek in the Hunter River region on the eastern side of the Liverpool Range (see comments below).

Comments: Specimens in the Hunter River drainage tentatively recognized as *Craterocephalus amniculus* present a problem: only 6 specimens have ever been collected, one from Bowmans Creek in 1976 and 5 from Glennies Creek in 1980. At this stage, it is not possible to determine whether the hardyhead populations are established in this

TABLE 2

Morphometric proportions and meristic counts of the holotype and 24 paratypes and 7 other specimens of Craterocephalus amniculus

Size and Range In SL	Holotype 40.0m SL	Paratypes and 7 other specimens 31 (25.8-44.2mm SL) Mean	Range	SD
Head	3.4	3.4	(3.3-3.6)	.08
H. max	4.5	4.4	(4.0-5.3)	.28
H. min	11.0	10.8	(9.9-11.9)	.55
Pec/anus	2.8	2.9	(2.6-3.1)	.12
Sn-OD1	2.0	2.0	(1.8-2.1)	.06
Sn-OD2	1.5	1.5	(1.4-1.5)	.05
Sn-OV	2.0	2.1	(2.0-2.2)	.07
Sn-TV	1.6	1.7	(1.6-1.8)	.06
Sn-OA	1.4	1.5	(1.4-1.5)	.05
Sn-TA	1.3	1.3		
In Head				
Eye	3.5	3.5	(3.0-3.9)	.25
Interorb.	2.9	2.9	(2.6-3.3)	.18
Postorb.	2.2	2.2	(2.0-2.4)	.09
In Eye				
Snout	1.0	1.0	(0.8-1.2)	.12
Premaxilla	1.0	1.0	(0.9-1.1)	.07
Lips	2.3	2.4	(2.2-2.6)	.12
Premax. process	1.2	1.2	(1.0-1.5)	.14
Scales				
Midlateral	39	40.6	(37-48)	3.00
Transverse	16	15.9	(14-18)	1.03
Predorsal	18	17.7	(16-20)	1.04
Interdorsal	6	6.4	(5-8)	0.63
Fin rays				
1st dorsal	7	6.2	(5-7)	.54
2nd dorsal	6	5.8	(5-7)	.48
Anal	7	6.5	(5-8)	.63
Pectoral	12	12.0	(11-14)	.78
Other				
Gill rakers	10	10.2	(9-11)	0.54
Posit. anus	B0.5	B0.3	(B0.5-F0.5)	0.51
OD1-TV	F6	F6.9	(F5-9)	1.03
OD1-TPec	B2	B1.5	(B3-F1)	1.09
OV-TPec	F0	F0.3	(B2-F2)	0.95
Vertebrae	34	*34.9	(33-36)	.88

* 15 specimens.

Abbreviations in morphometric/meristic tables: — H, height or body depth; — max, maximum; — min, minimum; — Pec, pectoral; — Sn, snout; — OD1, origin of first dorsal fin; — OD2, origin of second dorsal fin; — OV, origin of ventral fins; — TV, tips of ventral fins; — OA, origin of anal fin; — TA, insertion of last ray of anal fin; — TPec, tips of pectoral fin; — Interorb., interorbital; — Postorb., postorbital; — Premax. process, dorsal process of premaxilla; — Posit. anus, position of anus in relation to tips of ventral fins, expressed in a number of scales (B), behind, (F), in front of; — SL, standard length; — SD, standard deviation.

region or are a result of accidental or deliberate translocation. Systematic collecting in the Hunter River drainage system between Maitland and Muswellbrook N.S.W., over the last 5 years by both authors, has failed to find any more of this hardyhead in that region. A specimen from Glennies Creek, closely resembles members of the population now identified as *C. amniculus* in dentition, the shape of the maxilla and the length of the premaxillary symphysis. An electrophoretic analysis would confirm the status of the Hunter River hardyhead. Until such a study is made, the Hunter River hardyhead is considered to be indistinct from *C. amniculus*.

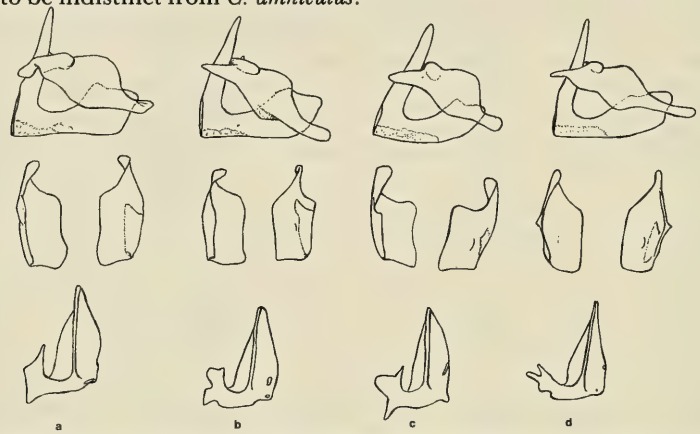

Fig. 2. Left maxilla and premaxilla; dorsal and ventral aspects of left nasal; left pelvic girdle, ventral aspect; of **a**) *C. amniculus*; **b**) *C. centralis*; **c**) *C. fluviatilis;* **d**) *C. eyresii.*

Craterocephalus centralis sp. nov.
(Fig 3)

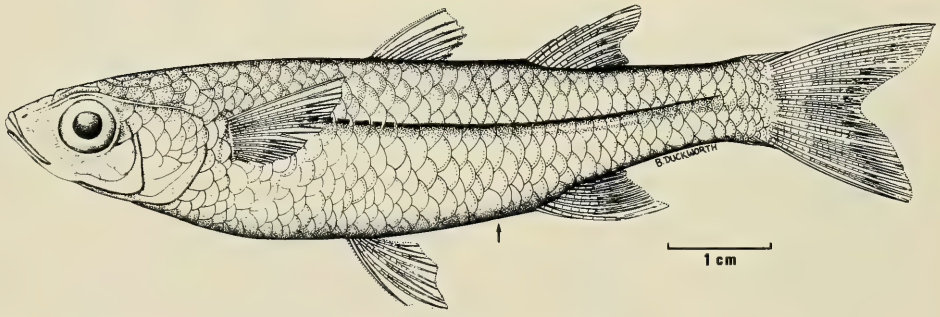

Fig. 3. Holotype of *Craterocephalus centralis*, AMS I.28888-001, 52.2mm SL.

Craterocephalus eyresii: Munro, 1958:102 (in part); Scott, Glover and Southcott, 1974:153 (in part).

Holotype: AMS I.28888-001 52.2mm SL. Finke River, Glen Helen Gorge, Northern Territory, 23°41′S, 132°40′E. Collected with 30m seine, in a shallow billabong (0.25-0.50m), overgrown with weeds and with a muddy bottom. Collected by L. E. L. M. Crowley and W. Ivantsoff, 13 September, 1987. For morphometrics and meristics of the holotype, see Table 4.

Paratypes: (29), AMS I.28874-001 (8, 43.8-56.1mm SL) Glen Helen Gorge, 23°42′S 132°40′E, collected 26 September 1983; AMS I. 28875-001 (1, 64.0mm SL) Salt Hole,

Finke River, Northern Territory, 24°02′S, 132°50′E, collected 26 September 1983; AMS I. 28875-002 (4, 34.3-43.9mm SL) Salt Hole, Finke River, Northern Territory, collected 19 September 1983; WAM P.29893.001 (2, 44.3-56.6mm SL) Pioneer Creek, 23°39′S 132°43′E, collected 28 April 1983; WAM P.29892.001 (4, 40.7-45.6mm SL) Palm Creek Crossing, 24°03′S 132°43′E, collected 20 December 1983; NTM S.12527-001 (4, 39.5-45.6mm SL) Finke River — Ellery Creek Junction, 24°06′S 132°48′E, collected 21 December 1983; NTM S.12528-001 (3, 40.9-51.9mm SL) Hermannsburg Mission, Rock Hole, Northern Territory, 23°57′S 132°46′E, collected 25 April 1983; UMMZ 214856 (2, 41.2-56.8mm SL) Finke River, 24°04′S 132°40′E collected 7 June 1983; AMNH 58689 (2, 46.0-52.3mm SL) as for UMMZ, collected 7 June 1983. All paratypes collected by D. Liddle. Material examined for osteology: AMS IA 24687.001 (4) as for holotype.

Diagnosis: A species of the atherinid genus *Craterocephalus*, superficially appearing to be closely allied to *C. eyresii*, but differing from that species in the following: transverse scales 10.5 (10-11); second dorsal fin rays 5 (4-6); anal fin rays 5.9 (5-7); gill rakers 10.2 (9-11). For a comparison of morphometric and meristic values of *C. centralis*, *C. amniculus*, *C. eyresii* and *C. fluviatilis*, see Table 2, 4, 5, 6. Differing osteologically from *C. eyresii*: in shape of premaxilla and nasal bones (see Fig. 2); in position of ventral wings of 5th ceratobranchial for attachment of *pharyngoclavicularis* muscle; in shape of basihyal; in length of posterior process of urohyal. Genetically distinct from *C. eyresii* in having fixed gene differences at two loci, high alternate allele frequencies at one locus (see Table 3). Having in common an allele at the GPI-2 locus only with *C. eyresii*.

Differing from all other species of genus *Craterocephalus* by the combination of the following: snout 0.9 (0.8-1.0); premaxilla 0.9 (0.8-1.0), both as proportion of diameter of eye; gill raker count 10.2 (9-11); transverse scale count: usually 4 (rarely 5) above midlateral band; in shape of medial process of pelvic girdle.

Description: A moderately robust fish, maximum known size 64.0mm SL. Mouth small but protractile; lips moderately thin. Gape restricted by labial ligament one third of way along mouth. Teeth in jaws sparse, minute, other bones edentulous. Premaxilla short, not reaching vertical through anterior edge of orbit; dorsal process of premaxilla barely reaching into interorbital space. Gill rakers tuberculate and widely spaced. Scales moderately large, strong, in even rows above midlateral stripe. Rows not always even below midlateral stripe. Scales on dorsum of head large, irregular; opercles scaled.

Colour: Live fish rich silvery-golden colour above prominent green/gold midlateral stripe; paler below; abdomen whitish. Opercles and eyes silver. Dorsum of head dark down to eye, pale silver below. Scales outlined above midlateral stripe; some scales below also showing reticulate pattern. Preserved fish from creamy yellow to light brown, depending on length of preservation. Eye silvery. Body with melanophores peppering scales above midlateral band, also forming reticulate pattern at edge of scales; reticulate pattern apparent below midlateral band in some specimens. Snout and lips peppered with melanophores. Dorsum of head very dark. Abdomen pale but with dark peritoneum visible through body wall, from origin of ventral fins, to anus. Pectoral, anal and dorsal fins with light dusting of melanophores. Ventral fins clear.

Etymology: *centralis* — indicating the species' provenance — Central Australia.

Distribution: This species of hardyhead is known only from the Finke River and bodies of water immediately associated with it. During times of dry weather or prolonged drought, the fish of this area seek refuge in pools formed by natural springs in the river bed.

Comments: *C. centralis* and *C. eyresii* are morphologically similar. *C. centralis* appears to be more robust but morphometric proportions for maximum body depth do not demonstrate any difference (*cf.* Tables 4, 5).

The close relationship of the specimens from the Finke River (*C. centralis*) and from Lake Eyre (*C. eyresii*), is further indicated by sharing of an allele (see Table 3) which is not found in any other species of hardyhead (Crowley, unpublished data). There is no doubt, however, that they are two distinct species since even at this locus (*GPI*-2), *C. eyresii* is polymorphic whilst *C. centralis* is monomorphic for the b allele. The absence of genetic flow between the populations indirectly confirms Kotwicki's (1989) belief that the Lake Eyre and the Finke River drainages are no longer contiguous.

TABLE 3

Enzyme loci which show allelic frequencies and fixed gene differences for four species of hardyheads, C. eyresii, C. centralis. C. amniculus *and* C. fluviatilis. *Alleles not present in these species are omitted*

Locus	Allele	*C. eyresii*	*C. centralis*	*C. amniculus*	*C. fluviatilis*
ADA	d	–	–	0.25	0.18
	e	–	–	0.75	0.82
	f	0.36	0.29	–	–
	g	0.64	0.71	–	–
CK	a	1.0	1.0	–	–
	b	–	–	–	1.0
	c	–	–	1.0	–
FUM	a	–	1.0	–	–
	b	0.54	–	1.0	1.0
	c	–	–	–	–
	d	0.46	–	–	–
GAPD	b	1.0	1.0	–	–
	c	–	–	1.0	1.0
GLDH	a	–	0.5	–	–
	b	–	0.5	0.2	–
	c	1.0	–	0.8	1.0
GOT-1	a	1.0	1.0	–	–
	c	–	–	1.0	1.0
GOT-2	b	–	–	1.0	1.0
	c	1.0	1.0	–	–
GPI-1	c	1.0	1.0	–	–
	d	–	–	0.8	0.9
	e	–	–	0.2	0.1
GPI-2	a	0.45	–	–	–
	b	0.55	1.0	–	–
	c	–	–	1.0	0.67
	d	–	–	–	0.33
IDH	a	–	–	1.0	1.0
	b	–	0.17	–	–
	c	1.0	0.83	–	–
MDH	a	0.39	0.31	–	–
	b	0.61	0.69	1.0	1.0
ME	b	0.75	0.3	–	–
	c	0.25	0.7	1.0	1.0
MPI	b	1.0	0.9	0.38	1.0
	c	–	0.1	0.62	–

The two loci for Glucose-phosphate isomerase (E.C. number 5.3.1.9) found in all *Craterocephalus* spp., support findings of Echelle and Echelle (1984) and Shaklee and Keenan (1986) who have found at least two loci for this enzyme in fish. This is contrary

to a report by Richardson *et al.* (1986) who suggested that only one locus for that enzyme was present in vertebrates.

Craterocephalus eyresii Steindachner, 1884
(Fig. 4)

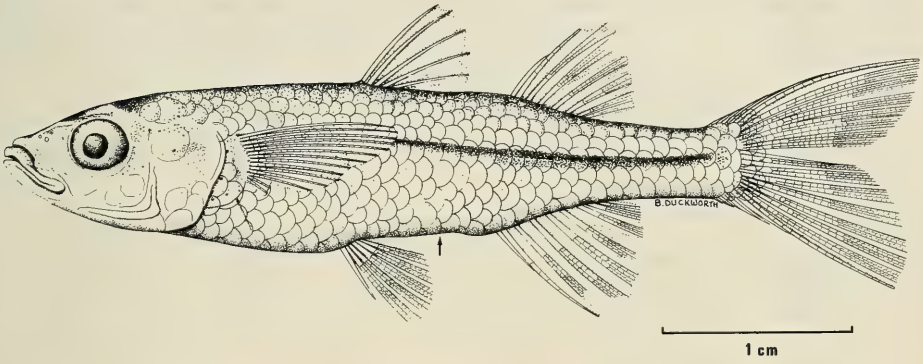

Fig. 4. Neotype of *Craterocephalus eyresii*; AMS I.28788-001, 40.0mm SL.

Atherinichthys eyresii Steindachner, 1884:1075, type locality: Coward and Strangways Springs (suggested by Jordan and Hubbs, 1919). Neotype designated herein.

Atherina interioris Zeitz, 1909:264 (*Nomen nudum*).

Craterocephalus eyresii: McCulloch and Waite, 1918:43; Jordan and Hubbs, 1919:45; McCulloch, 1929:109; Whitley, 1957:15; Munro, 1958:102; Scott, 1962:136: Scott, Glover and Southcott, 1974:153 (in part); Ivantsoff, 1978:245 (in part); Merrick and Schmida, 1984:145 (in part).

Craterocephalus fluviatilis: (not of McCulloch), Ivantsoff, Crowley and Allen 1987:174.

Designated Neotype: AMS I.28788-001 (40.0mm SL), collected by pole-seine at Strangways Springs, South Australia 29°09′S 136°34′E. Collected by W. Ivantsoff and L. E. L. M. Crowley, 12th June 1985. The designation of the neotype is strictly defined in Article 75 of International Code of Zoological Nomenclature (1985). The circumstance admitted (b) (I-III) and the qualifying conditions (d) (1-6) allow the designation in exceptional circumstances. As *C. eyresii* is now known to be a complex of four species, the designation of the neotype is considered to be essential.

Material examined: MQU WI-356 (20, 28.1-51.2mm SL), as for designated neotype; AMS I.13662 (10, 34.9-43.3mm SL) Strangways Springs. Additional material examined: MQU I-335 (4) Gregory Creek, 29°45′S 137°19′E; SAM F3545 (2) Johnsons No. 3 Bore 29°32′S 136°14′E; SAM F3958 (2) Lake Eyre 29°20′S 137°20′E; SAM F3986 (2) Peakes Bore, South Australia; SAM F4207 (2) Frome Creek, 29°19′S 137°58′E; SAM F4218 (2) Emu Creek 29°41′S 136°18′E; NMV A6159 (5) Lake Callabonna 29°40′S 140°01′E. Material examined for osteology: MQU IA 170 (4, 32.0-37.2mm SL) Strangways Springs.

Diagnosis: A freshwater species of the genus *Craterocephalus* most closely related to *C. centralis* but differing from that species in the following: snout to insertion of last ray of anal fin in SL 1.3 (1.2-1.3); transverse scale count 12.2 (11-14); predorsal scale count 16.3 (13-20); second dorsal fin rays 5. 8 (5-7); anal fin rays 6.5 (5-8); 5 or more scales above midlateral stripe, 6-8 scales below; in shape of nasal bone (see Fig. 2); in position of ventral wings of 5th ceratobranchial for attachment of *pharyngoclavicularis* muscle; in

shape of basihyal; in length of posterior portion of urohyal. Differing genetically from *C. centralis* at two loci (see Table 3).

TABLE 4

Morphometric proportions and meristic counts for the holotype and 30 paratypes of C. centralis

Size and Range In SL	Holotype 52.2mm SL	Paratypes 30 (34.3-64.0mm SL) Mean	Range	SD
Head	3.5	3.4	(3.2-3.7)	.15
H. max	4.0	4.3	(3.6-4.9)	.34
H. min	9.7	9.4	(8.6-10.8)	.56
Pec/anus	2.6	2.8	(2.4-3.0)	.13
Sn-OD1	2.0	2.0	(1.9-2.2)	.06
Sn-OD2	1.4	1.4	(1.4-1.5)	.04
Sn-OV	2.1	2.1	(1.9-2.2)	.07
Sn-TV	1.6	1.6	(1.5-1.7)	.04
Sn-OA	1.4	1.4	(1.4-1.5)	.03
Sn-TA	1.3	1.3		
In Head				
Eye	3.4	3.7	(3.4-4.1)	.17
Interorb.	3.0	2.9	(2.6-3.1)	.13
Postorb.	2.3	2.2	(2.0-2.3)	.07
In Eye				
Snout	1.0	0.9	(0.8-1.0)	.07
Premaxilla	0.9	0.9	(0.8-1.1)	.08
Lips	2.3	2.4	(2.0-2.7)	.19
Premax. process	1.1	1.3	(1.1-1.5)	.12
Meristics				
Scales				
Midlateral	32	31.9	(31-33)	.63
Transverse	10	10.5	(10-11)	.51
Predorsal	15	15	(13-16)	.98
Interdorsal	6	5.6	(4-7)	.68
Fin rays				
1st dorsal	6	5.8	(5-6)	.43
2nd dorsal	6	5.0	(4-6)	.61
Anal	6	5.9	(5-7)	.61
Pectoral	12	12.4	(11-13)	.67
Other				
Gill rakers	11	10.2	(9-11)	.57
Posit. anus	B2	B0.5	(B0-2)	.65
OD1-TV	F4	F4.6	(F3.5-6)	.66
OD1-TPec	B1.5	B1.4	(B0-4)	.90
OV-TPec	F1	F0.7	(B2-F2)	.72
Vertebrae	34	*32.7	(32-34)	.69

* 17 specimens.

Distinguished from all other species of *Craterocephalus* by the combination of: transverse scale count 12.2 (11-14); minimum body depth in SL 10.1 (8.3-12.0); unique in having the GPI-2 a allele but sharing GPI-2 b allele with *C. centralis*.

Description: Moderately robust fish, but seemingly varying in body depth with age. Mouth protractile; lips moderately fleshy. Gape restricted by fusion of lips from about half to two thirds way along premaxilla. Teeth in jaws small, other bones edentulous. Premaxilla short, not reaching vertical through anterior edge of orbit; dorsal process of premaxilla just reaching interorbital space. Gill rakers short, less than half diameter of pupil, occasionally tuberculate. Scales moderately small, strong, not always in even rows above or below midlateral stripe; circuli obvious on all scales. Scales on dorsum of head irregular, usually larger than body scales; opercles scaled.

TABLE 5

Morphometric proportions and meristic counts for the designated neotype and 29 specimens of C. eyresii *from Strangways Springs (suggested type locality by Jordan and Hubbs, 1919)*

Size and Range In SL	Neotype 40.0mm SL	Other specimens 29 (28.1-51.2mm SL) Mean	Range	SD
Head	3.3	3.4	(3.2-3.8)	.18
H. max	4.1	4.4	(3.8-5.3)	.30
H. min	9.7	10.1	(8.3-12.0)	.77
Pec/anus	2.9	2.8	(2.5-3.1)	.12
Sn-OD1	2.0	2.0	(1.9-2.1)	.07
Sn-OD2	1.4	1.4	(1.3-1.5)	.05
Sn-OV	2.1	2.1	(1.9-2.3)	.08
Sn-TV	1.6	1.6	(1.5-1.8)	.06
Sn-OA	1.5	1.4	(1.4-1.5)	.05
Sn-TA	1.3	1.3	(1.2-1.3)	.04
In Head				
Eye	3.8	3.7	(3.2-4.3)	.23
Interorb.	2.9	3.0	(2.7-3.3)	.16
Postorb.	2.3	2.2	(2.1-2.4)	.07
In Eye				
Snout	0.9	0.9	(0.7-1.1)	.09
Premaxilla	0.8	0.9	(0.7-1.1)	.09
Lips	2.6	2.6	(2.2-3.0)	.23
Premax. process	1.1	1.2	(0.9-1.5)	.12
Meristics				
Scales				
Midlateral	32	32.2	(30-34)	0.94
Transverse	12	12.2	(11-14)	0.89
Predorsal	16	16.3	(13-20)	1.64
Interdorsal	7	6.1	(4-7)	0.77
Fin rays				
1st dorsal	5	5.9	(4-7)	.83
2nd dorsal	5	5.8	(5-7)	.62
Anal	6	6.5	(5-8)	.71
Pectoral	13	12.5	(12-14)	.61
Other				
Gill rakers	11	11.1	(10-12)	0.68
Posit. anus	F0.5	B0.4	(F1-B1.5)	0.54
OD1-TV	F6	F5.4	(F3-8)	1.12
OD1-TPec	F1	B0.3	(B3-F2)	1.33
OV-TPec	F2	F1.4	(0-F3)	0.94
Vertebrae	33	*32.3	(31-34)	0.83

* 17 specimens.

Colour: Live specimens usually bright yellow with distinct silvery midlateral stripe. Opercles and abdomen iridescent green or silvery. Fins clear to yellowish. Preserved specimens from pale yellow to dark brown, depending on method and length of preservation. Eyes dark. Midlateral stripe either silvery or very dark, thin from origin of pectoral fin but becoming wider caudally and ending in series of small spots. Scales above midlateral stripe speckled with melanophores but reticular pattern not obvious; melanophores sparsely scattered below midlateral stripe. First and second dorsal, anal and pectoral fins with rows of melanophores along spines and rays; ventral fins clear.
Distribution: The species is found in the Lake Eyre Drainage. It has been collected from the Frome River and other rivers, streams and bores of South Australia. It appears that sufficient numbers survive dry seasons in refuge areas, dispersing and breeding rapidly in favourable conditions, only to die out again due to increasing salinity and evaporation of the water (see Ruello, 1976).
Comments: The integrity of the Lake Eyre Drainage is well discussed by Kotwicki (1989). From that study, it appears that the system is isolated from other drainage systems. These data are in agreement with the findings presented. *C. eyresii* is genetically isolated from the Finke River *C. centralis*, a river which even in the highest flood years does not reach Lake Eyre. The drainages to the south east are also not connected with the Lake Eyre Drainage System (Kotwicki, 1989). The separation of these drainages has allowed speciation to occur, resulting in close but distinct species, *C. fluviatilis* in the lower reaches of the Murray-Darling and *C. amniculus* in the higher reaches of the same drainage. A full biogegraphic review of the genus *Craterocephalus* is in preparation by the authors.

Craterocephalus fluviatilis McCulloch, 1913

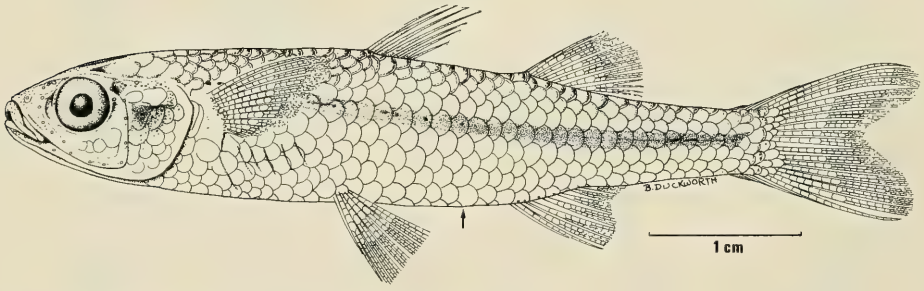

Fig. 5. Specimen of *Craterocephalus fluviatilis*; NMV A6161, 49.7mm SL.

Craterocephalus eyresii: Scott, Glover and Southcott 1974:153 (in part); Ivantsoff, 1978:245 (in part); Lake, 1978:41 (in part); Cadwallader and Backhouse, 1983:94 (in part); Merrick and Schmida, 1984:145 (in part); Ivantsoff, Crowley and Allen, 1987a:174.
Holotype Examined: AMS I.12456 (1, 47.2mm SL), North Yanko Creek, Narrandera, N.S.W.
Paratypes Examined: AMS I.12457 (2, 27.8-46.9mm SL), as for holotype. Remaining paratypes identified as *C. stercusmuscarum fulvus* (Ivantsoff *et al.*, 1987a).
Additional Material Examined: NMV A6157 (13) Lake Wandella, Vic., 35°45′S 143°53′E; NMV A6161 (14), Lake Hawthorn, Mildura, Vic., 34°12′S 142°06′E; MQU I.470 (5), Lake Hawthorn, Mildura, Vic. Material examined for osteology: MQU IA 73-4 (5) Lake Bonney, South Australia, 37°45′S 140°20′E; MQU IA 99 (2)

North Yanko, New South Wales, 34°52′S 146°18′E; MQU IA 100 (1) Murray River, N.S.W. 34°11′S 142°10′E.

Diagnosis: Moderately small fish most closely related to *Craterocephalus amniculus* and *C. eyresii* but differing from those species by a combination of the following: least body depth 11.6 (10.6-12.6) in SL; eye 3.4 (3.2-3.9); interorbital 3.0 (2.7-3.4) both in head; premaxillary process 1.4 (1.1-2.1) in eye. Midlateral scale count 33.1 (31-35); transverse scale count 10.9 (10-12); position of anus 1.2 (0-2) scales behind tips of ventral fins; in shape of basisphenoid; position of dorsal flange of 5th ceratobranchial. Differing: from *C. eyresii* in size and length of urohyal; in shape of medial process of pelvic girdle; from *C. amniculus* in shape of anterior process of maxilla (see Fig. 2). Differing genetically from *C. amniculus* at a single locus (CK); and from *C. eyresii* at 8 loci (ADA, CK, GAPD, GOT-1, GOT-2, GPI-1, GPI-2, IDH). For genetic differences and similarities between species, see Table 3.

Distinguished from all other members of the genus by a combination of the following: least body depth 11.6 (10.6-12.6); distance from origin of pectoral to anus 2.9 (2.6-3.2), both as proportion of SL; midlateral scale count 33.1 (31-35); transverse scale count 10.9 (10-12); predorsal scale count 14.3 (12-17); position of anus 1.2 (0-2) scales behind tips of ventral fins; origin of first dorsal 4.9 (3.5-6.5) scales in front of tips of ventral fins; single row of small, inward pointing teeth in upper and lower jaws; anterior arms of lateral ethmoids not fusing strongly to vomer as in other species.

Description: Small, moderately deep bodied freshwater fish, maximum size known 60.0mm SL. Most similar superficially to *Craterocephalus eyresii* as suggested by McCulloch (1913). Mouth small, protrusible, lips not thick, gape restricted by labial ligament from one third to half way along premaxilla. Teeth small, in single row and restricted to anterior part of both jaws. Premaxilla not reaching vertical through anterior margin of orbit; dorsal process of premaxilla not reaching interorbital space. Body scales small, thin, deciduous, almost circular, with circuli obvious and complete. Opercle, preopercle and dorsum of head with larger scales; scales on dorsum of head reaching to anterior margin of orbit. Gill rakers on lower ramus of 1st gill arch, short, tuberculate, last 2-3 slightly longer.

Colour: Live specimens varying from silver to dark golden dorsally with silver midlateral stripe; abdomen always pale with silvery iridescent sheen. Opercles, eye, bright silver; dorsum of head darker than snout. Fins clear to creamy. Preserved specimens pale creamy-yellow to light tan with midlateral band not prominent; melanophores forming light reticulate pattern on scales above midlateral band; scales below unmarked. Dorsum of head, snout and chin lightly peppered with melanophores; opercle with distinct triangular dark patch. Ventral contour of spots from end of anal fin to procurrent rays of caudal fin. Dorsals, anal and caudal fins with some melanophores outlining spines and rays; pectoral and ventral fins clear.

Distribution: According to McCulloch (1913), this species was reported to have a wide distribution in the upper Murray River Drainage (Yanko Creek, Murrumbidgee River as far east as Cooma). The occurrence of *C. fluviatilis* in northern tributaries of the Darling is doubtful, despite the reports of its presence in that river (McCulloch, 1913). Its present range appears to be restricted to Victoria, in some small lakes associated with the Murray River, where it is presently abundant. Recent collecting in the Murray River, south of Renmark and in Lake Bonney, South Australia, failed to yield any specimens, where previously, this species had been reported by Lloyd & Walker (1986) from five sites in the lower Murray, in 1976.

Comments: Although McCulloch was aware that specimens from the Namoi and Barwon Rivers had 7 rows of scales whilst of those from Narrandera, 3 had 10, two had 8 and one had 7 transverse scale rows, he described the populations as a single species.

Ivantsoff *et al.* (1987a) concluded that the type material of *C. fluviatilis*, McCulloch (1913) included two separate species which they then identified as *C. eyresii* and *C. stercus-muscarum fulvus*. Clearly, specimens from Narrandera and the Namoi and Barwon Junction with 7-8 transverse scale rows are *C. s. fulvus*; the three specimens with 10 scale rows are *C. fluviatilis*.

TABLE 6

Morphometric proportions and meristic counts for the holotype and 2 paratypes (McCulloch's 1913 material) and 33 other specimens of C. fluviatilis

Size and Range In SL	Holotype 47.6mm SL	2 paratypes and 33 other specimens 35 (24.1-58.4mm SL) Mean	Range	SD
Head	3.8	3.5	(3.1-4.0)	.20
H. max	4.8	4.6	(4.0-5.1)	.28
H. min	12.5	11.6	(10.6-12.6)	.61
Pec/anus	2.9	2.9	(2.6-3.2)	.16
Sn-OD1	2.0	2.1	(1.9-2.2)	.06
Sn-OD2	1.5	1.5	(1.4-1.5)	.03
Sn-OV	2.1	2.1	(2.0-2.3)	.10
Sn-TV	1.7	1.7	(1.6-1.8)	.06
Sn-OA	1.5	1.5	(1.4-1.6)	.04
Sn-TA	1.3	1.3	(1.1-1.3)	.04
In Head				
Eye	3.5	3.4	(3.2-3.9)	.19
Interorb.	2.8	3.0	(2.7-3.4)	.18
Postorb.	2.2	2.3	(2.2-2.4)	.08
In Eye				
Snout	1.1	1.0	(0.8-1.5)	.12
Premaxilla	1.2	1.0	(0.9-1.4)	.12
Lips	2.2	2.4	(2.1-2.7)	.14
Premax. process	1.4	1.4	(1.1-2.1)	.27
Meristics				
Scales				
Midlateral	32	33.1	(31-35)	0.84
Transverse	10	10.9	(10-12)	0.59
Predorsal	15	14.3	(12-17)	1.28
Interdorsal	6	5.7	(5-7)	0.60
Fin rays				
1st dorsal	6	5.8	(4-7)	.79
2nd dorsal	6	6.2	(5-8)	.71
Anal	7	7.2	(6-9)	.61
Pectoral	—	11.9	(11-13)	.52
Other				
Gill rakers	11	10.8	(10-12)	0.73
Posit. anus	0	B1.2	(0-B2)	0.78
OD1-TV	F6	F4.9	(F3.5-6.5)	0.90
OD1-TPec	B0.5	B1.6	(F1-B3.5)	1.04
OV-TPec	0	F0.2	(B2-F2)	1.06
Vertebrae	34	34	(33-35)	0.59

* 18 specimens.

McCulloch's (1913) records of distribution of *C. fluviatilis* must now be considered equivocal since other specimens which he attributed to this species may be either *C. s. fulvus* or *C. amniculus*.

Discussion

Morphological and osteological conservatism of atherinids appears to be commonplace. Fossil fish from the Miocene (Messinian) deposits in northern Italy are similar to the extant species *Atherina boyeri* (Gaudant, 1981: ". . . les athérines de Cherasco présentent beaucoup d'affinités avec *Atherina (Hepsetia) boyeri* Risso"). Pliocene atherinids from Arizona (Todd, 1976) are not very different from the extant species of *Colpichthys*. Harman *et al.* (1982) consider that there is probably only one species of *Pranesus* (=*Atherinomorus*, see Whitehead and Ivantsoff, 1983) in the Pacific and Indian Oceans, rather than a much larger number that has been described over the last hundred and fifty years. Bamber and Henderson (1985) on the basis of their meristic and morphological studies concluded "that *A. presbyter* and *A. boyeri* reflect the tails of a continuum. . . . It is best to consider the single species *Atherina boyeri* . . .". Whilst it might be considered that morphologically *C. centralis* and *C. amniculus* represent the "tails of a continuum" (*sensu* Bamber and Henderson, 1985), genetically this appears to be unlikely. The fixed gene differences between the populations from the Finke River (which rarely, if ever, flows into Lake Eyre — Kotwicki, 1989), and the populations from the Lake Eyre drainages, indicate that speciation has occurred.

Similarly, despite the presence of only a single fixed gene difference between *C. fluviatilis* and *C. amniculus*, the differences in morphology and osteology indicate that these also are separate species. Flooding in the Murray-Darling drainage system has been well documented (Russell, 1892) allowing interbreeding in the recent past; but a single fixed gene difference between populations in contiguous waterways indicates that interbreeding no longer occurs.

Speciation of freshwater fish in Australia is considered to be recent, according to some workers (Whitley, 1959; Allen and Cross, 1982; Merrick and Schmida, 1984). Extrapolating from the data of Echelle and Echelle (1984) it would appear that, whilst *C. eyresii*, *C. centralis* and *C. fluviatilis* are morphologically and osteologically conservative, these species are more genetically divergent than the morphologically conservative atherinid species flocks of *Chirostoma*, from the Mesa Central (Mexico), which Echelle and Echelle (1984) suggested date only from Plio/Pleistocene. Higher numbers of fixed gene differences (see Table 3) between populations from either side of the Flinders and Barrier Ranges, all previously considered to be *C. eyresii*, indicate that separation has been longer than is found between *Chirostoma* species.

Reasons for the absence of small native species from previously known areas (e.g. the hardyheads from the Hunter and Murrumbidgee Rivers) are a matter of conjecture. There is a paucity of information on whether small endemic fishes can compete successfully with introduced species; if they can withstand the changes due to agricultural and pastoral practices; or how they react to the use of fertilizers, weedicides and insecticides. Studies on the decline of endemic species exist (e.g. Cadwallader, 1978) but these tend to apply to larger and commercially important fish.

Extinction of Australian aquatic organisms has become a matter of concern in recent years. A report by Michaelis (1985) lists the threatened fishes of inland waters of Australia and includes some useful biological and geographical data on each. The proceedings of the conference on Australian threatened fishes (Harris, 1987) propose strategies to protect and conserve the native inland fishes.

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Analysis of the Frequency of *Lechriodus intergerivus* Tyler (Anura: Leptodactylidae) in Oligo-Miocene Local Faunas of Riversleigh Station, Queensland

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TYLER, M. J., HAND, S. J., & WARD, V. J. Analysis of the frequency of *Lechriodus intergerivus* Tyler (Anura: Leptodactylidae) in Oligo-Miocene local faunas of Riversleigh Station, Queensland. *Proc. Linn. Soc. N.S.W.* 112 (2), 1990: 105-109.

Lechriodus intergerivus Tyler, 1989 occurs in large numbers in Oligo-Miocene fossil deposits on Riversleigh Station, in northwestern Queensland, dominating the Riversleigh frog faunas in which it occurs. The abundance of *L. intergerivus* in the Riversleigh fossil deposits does not appear to reflect either dry condition aggregates or breeding congregations, but rather the relative abundance of this species in local frog faunas. The frequency of *L. intergerivus* in the Riversleigh sites appears to broadly correlate with the age of the sediments in which it occurs: the proportion of *L. intergerivus* is higher in Riversleigh's early to middle Miocene sites (up to 80.8% of frogs) than in middle to early late Miocene deposits (as low as 35.5%). Changes in forest habitat in the Riversleigh area during the Miocene may have contributed to the observed decline in numbers of *L. intergerivus*.

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INTRODUCTION

Lechriodus intergerivus Tyler (1989) was described from 190 ilia recovered from fossil-rich Oligo-Miocene freshwater limestone deposits on Riversleigh Station in northwestern Queensland. It represents the second Tertiary leptodactylid (myobatrachid) reported from Australia. At the time of the preparation of the description 397 frog ilia had been recovered from the Riversleigh deposits, of which 50% represented *L. intergerivus*.

Subsequent preparation of more of the Riversleigh Oligo-Miocene limestone in the School of Biological Science at the University of New South Wales has produced many more frog specimens that confirm this observation. The total number of ilia recovered has doubled to 777, of which 420 are *L. intergerivus*, (54% of the total).

Given that there are at least 15 frog species in the Riversleigh Oligo-Miocene faunas (Tyler, unpubl.), a variety of reasons could be postulated to explain the prevalence of this species in the Riversleigh fossil record. Here we document the incidence across the ten sites where we consider sample sizes to be adequate, and explore the palaeoenvironmental implications of the observations.

INCIDENCE

In a sequence of fossil deposits on Riversleigh, which spans the last 25 million years, more than 100 local faunas or fossil assemblages are now recognized (Archer *et al.*, 1989). The majority of these local faunas are of Oligo-Miocene age, i.e. approximately 15-25 million years old. *Lechriodus intergerivus* has been recorded from 20 of Riversleigh's Oligo-Miocene local faunas. At each of ten of these sites at least 15 frog ilia have been recovered. The incidence of *L. intergerivus* at those ten is expressed in Fig. 1 as a

percentage of ilia recovered from each site. The lowest incidences occur at Gag and Henk's Hollow Sites (35.5 and 35.8% respectively) and the highest at Wayne's Wok Site (80.8%).

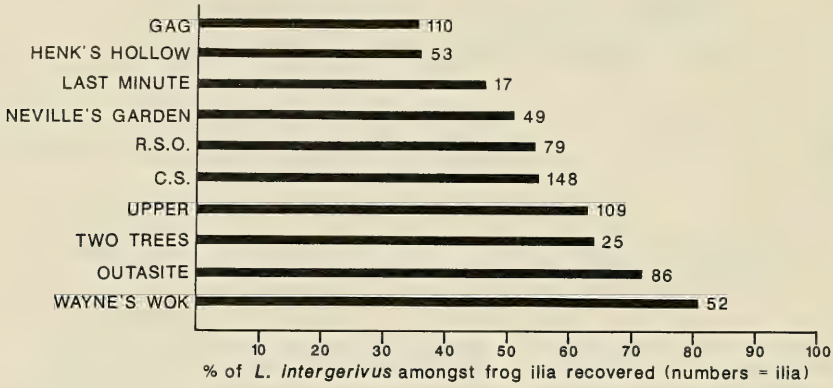

Fig. 1. Incidence of *Lechriodus intergerivus* at ten sites in the Riversleigh Oligo-Miocene faunas.

Archer *et al.* (1989) have identified three primary intervals of Oligo-Miocene deposition at Riversleigh which they define as Systems A-C, System A being late Oligocene to early Miocene in age, System B possibly early to middle Miocene and System C middle to early late Miocene in age. The frequency of *L. intergerivus* in these sites appears to broadly correlate with the age of the sediments in which it occurs. For at least Riversleigh's Systems B and C, the older the local fauna, the higher the proportion of *L. intergerivus* among its frogs. Wayne's Wok, Outasite, Upper, CS and RSO Sites occur within Riversleigh's Sytem B sediments, while Last Minute, Henk's Hollow and Gag Sites are part of the younger System C (Archer *et al.*, 1989). *Lechriodus intergerivus* has not been recorded from System A sites.

There are two notable exceptions to the observed pattern. From Two Trees Site, a System C site, a relatively high proportion of *L. intergerivus* has been recovered. From Neville's Garden Site, the proportion of *L. intergerivus* retrieved is relatively low, yet the deposit is interpreted to be among the oldest of System B sites (Archer *et al.*, 1989).

Discussion

Two particular aspects of these observations merit discussion: the overall high incidence of *L. intergerivus* in all 10 sites; and the variation in incidence between sites.

Unless *L. intergerivus* was in some way selectively favoured for fossilization by an unknown process, it would appear that its predominance at the sites is not an artefact, but a reflection of its relative abundance.

Two behavioural characteristics of frogs can lead to high densities of single species at a particular site: localized breeding congregations, and aggregations to reduce water loss during dry conditions.

Non-breeding aggregations have been documented in numerous leptodactylid and hylid species, e.g. *Limnodynastes fletcheri* (Tyler, 1976), *Taudactylus diurnus* (K. R. McDonald, pers. comm.), *Litoria caerulea* and *L. rubella* (Slevin, 1955) and *L. coplandi* (Miles, 1988).

Considering the possibility that the high numbers were the result of aggregation during dry conditions, the palaeoenvironment of the late Oligocene to middle Miocene of the Riversleigh area is interpreted by Archer *et al.* (1989) to have been lush, lowland

rainforest with a partially open understory, and hence dry conditions as such are unlikely to have led to aggregations of this single species.

Within our experience, dense breeding populations in Australia are almost inevitably composed of mixed species. Nevertheless predominance of any one species could on occasions amount to perhaps one-third of the mixed population (at the lower end of the range that we report). *Litoria chloris* is an example of a species that will breed in shallow water in enormous numbers in the absence of any other species (McDonald, Seymour, Davies and Tyler, unpubl. 1976).

Extant species of *Lechriodus* are moderate sized frogs restricted to temperate and subtropical rainforests of New Guinea (three species) and northeastern New South Wales and southeastern Queensland (one species: *L. fletcheri*). Biological data on extant *Lechriodus* species are confined to details of the life history of *L. fletcheri*. Eggs are deposited in foam nests often hidden from direct light. The deposition site commonly is small bodies of water with limited food, and the tadpoles are carnivorous and often cannibalistic (Moore, 1961; Martin, 1967; Tyler unpubl.). Perhaps as a consequence of the spatial separation of the egg clumps, *L. fletcheri* does not form large breeding congregations. The likelihood of simultaneous fossilization of breeding congregations not explaining the dominance of *L. intergerivus* at Riversleigh Station, is further supported by the presence of diverse sizes in the samples, which are therefore not confined to adults, as would occur in a breeding congregation.

Considering the differences in density per site, it is possible that progressive changes in climate could account for most of the observed changes. As noted above, Archer *et al.* (1989) interpret the palaeoenvironment of the Riversleigh area during the Oligo-Miocene to have been rainforest. Subsequent and progressive drying and cooling of northern Australia during the remainder of the Tertiary and Quaternary brought dramatic changes to the area. By Pliocene-Quaternary time, Riversleigh species-level and family-level diversity had fallen. This is most evident among mammals, and appears to reflect the collapse of local rainforest communities and their replacement by open forest savannah habitats (Archer *et al.*, 1989).

Evidence from the Riversleigh faunas, and other northern Australian fossil faunas such as the Northern Territory's Bullock Creek Local Fauna and Alcoota Local Fauna (Woodburne *et al.*, 1985), suggests that these changes began as early as the middle to late Miocene, i.e. during Riversleigh's Systems B-C time.

The decline in numbers of *L. intergerivus* in Riversleigh's System C deposits may reflect a decline in moist, rainforest habitat, or at least a particular component of that habitat, resulting from broad changes in forest and animal communities occurring across northern Australia during the middle and late Miocene.

It is also apparent that the immediate depositional environment of a fossil site influences its faunal composition. At Riversleigh, many different depositional mechanisms appear to have been responsible for producing the variety of Oligo-Miocene sediments observed.

Some deposits evidently accumulated inside caves, others outside in the forest in shallow or deep water. Depositional environments at most of the sites containing *Lechriodus* are interpreted to have been broadly similar: relatively small, spring-fed, lime-rich pools occurring in rainforest-covered karst country. Upper Site is probably the best studied of this kind of Riversleigh deposit and also one of the richest. Animals recovered from 1.5 tonnes of Upper Site limestone include 64 species of mammals, as well as diverse assemblages of birds, reptiles, frogs, fish and even invertebrates (Archer *et al.*, 1989). Thirteen species of frogs have been recorded from Upper Site: six leptodactylid species (*L. intergerivus*, *Crinia* sp., two species of *Kyarranus* and two *Limnodynastes*) and

eight hylid species (*Litoria* spp.) (Archer *et al.*, 1989). Conditions at such sites evidently favoured *L. intergerivus*, which at Upper Site comprises 63% of the frog fauna.

On the other hand, *L. intergerivus* is noticeably absent from a number of Oligo-Miocene deposits interpreted to have accumulated in large or deep pools. For example, this species has not yet been found at sites such as Ringtail, Bob's Boulders, Crusty Meat Pie and Quentin's Quarry, relatively well-sampled System C deposits interpreted to have been deep pools supporting large individual fish, crocodiles, turtles and sometimes platypuses. Nor has it been found in System A sites. The palaeoecological model proposed by Archer *et al.*, (1989) for System A deposits (e.g. Site D and equivalents such as Sticky Beak and White Hunter Sites) is a large, spring-fed lake, fringed by lush rainforest, that filled the central basin of the Riversleigh area. Perennial streams or periodic rushes of surface water may have fed the lake from surrounding forested terrain. Today, *L. fletcheri* chooses small bodies of water in which to deposit its eggs. That water depth might have always been an important limiting factor for *Lechriodus* is an hypothesis testable by continued study of these sites and their faunas.

For many other deposits, understanding about local conditions is still rudimentary. This is certainly true for both Neville's Garden Site and Two Trees Site. Neville's Garden appears to have provided less suitable habitat for *L. intergerivus* than other System B sites, while Two Trees Site provided far more suitable conditions than all other System C sites. Preliminary investigations of these sites and their faunas suggest that the Neville's Garden deposit accumulated in a pool just outside a cave (the depth and extent of this pool is as yet unknown), while the Two Tree deposit remains an enigma. The latter is associated with a thick bed of horizontally laminated travertine and, more curiously, it contains the potoroid marsupial *Bettongia moyesi*, the only occurrence of the genus in the Tertiary record (Flannery and Archer, 1987). Further study of these sites and their faunas will be important in identifying factors affecting Riversleigh's fossil frog communities and defining the microhabitat requirements for *L. intergerivus*.

In summary, the predominance of *L. intergerivus* in many of Riversleigh's Oligo-Miocene fossil deposits appears to reflect its relative abundance in local frog faunas, rather than breeding congregations or aggregations resulting from dry conditions. The frequency of *L. intergerivus* in the Riversleigh deposits correlates with two factors: water depth and age of deposit. Shallow (rather than deep) water environments appear to have been the preferred habitat for *Lechriodus intergerivus*. Within this habitat *L. intergerivus* is more abundant in older rather than younger Riversleigh deposits, the marked decline in the species' abundance being attributed here to changes in forest habitat in the Riversleigh area during the Miocene.

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Rare and Biogeographically Significant Vascular Plant Species of the Eden Region, South-eastern New South Wales: a Listing for the 'Fine-Filter' Approach

D. A. KEITH

KEITH, D. A. Rare and biogeographically significant vascular plant species of the Eden region, south-eastern New South Wales: a listing for the 'fine-filter' approach. *Proc. Linn. Soc. N.S.W.* 112 (2), 1990: 111-132.

Approaches to conservation based on high levels of biological organization must be complemented by a species level approach if rare and other significant species are to be adequately reserved. A listing of rare and biogeographically significant vascular plant species has been compiled for the Eden region using explicit selection criteria derived from accepted conservation goals. Thirteen species were endemic to the region, 40 rare or threatened in an Australia-wide context, 34 uncommon throughout their distribution, 6 restricted outside the Eden region, 279 uncommon within the region but common elsewhere, 8 depleted in the wild, 183 reaching their geographical limit of distribution in the Eden region, 23 represented in the Eden region by geographically disjunct populations, and 8 represented by ecologically disjunct populations. Species in these categories may be given different priorities for conservation, depending on the level of representation required.

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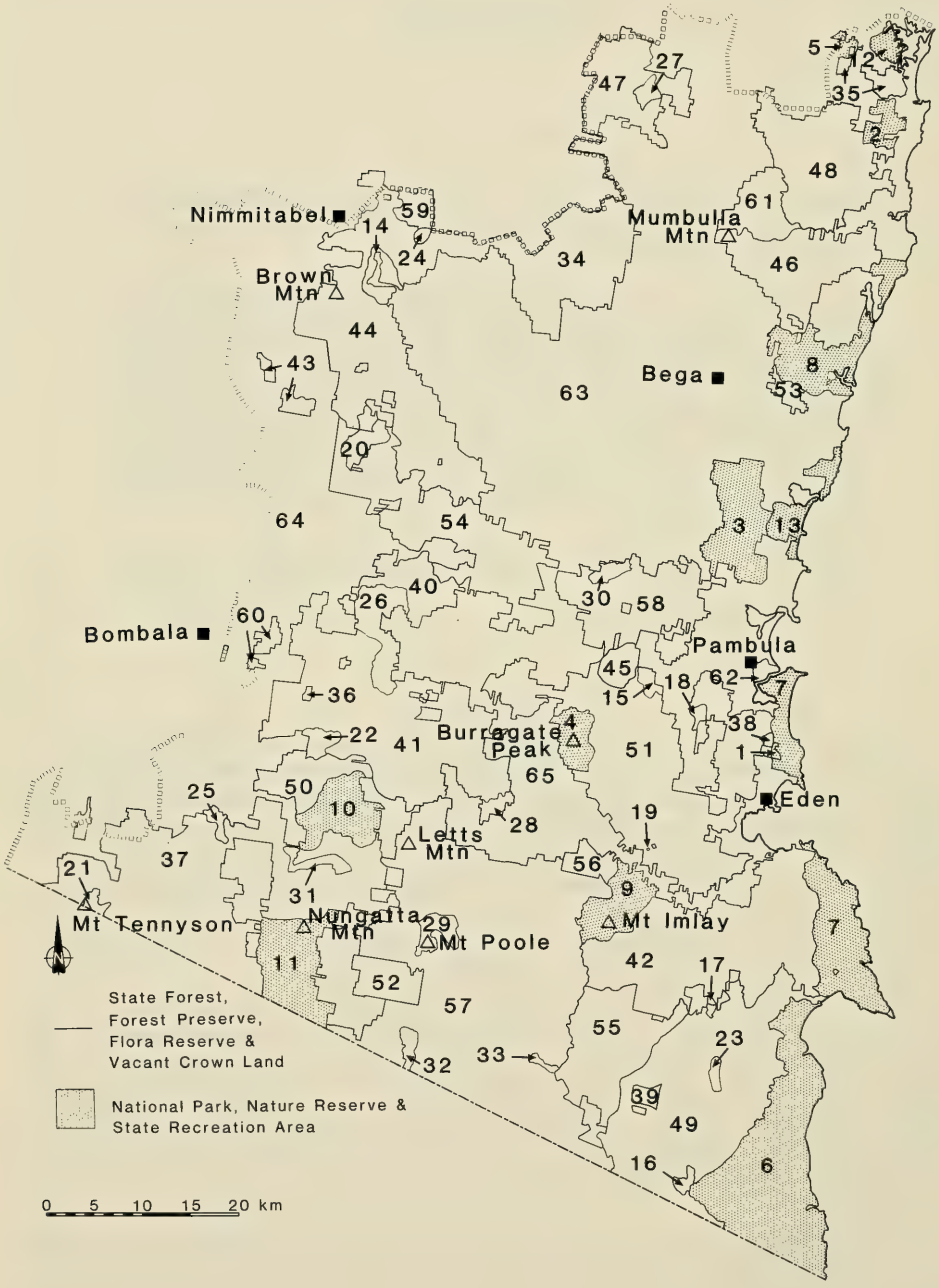
KEY WORDS: Rare plants, conservation, representative, coarse filter, fine filter, Eden.

INTRODUCTION

Conservation of representative samples of biota in reserves is an important aspect of conservation planning (Austin and Margules, 1986). If a reserve system is to represent the full range of a regional biota, reserves must contain samples of all species occurring in the region. The task of planning a representative reserve system is made difficult by the vast numbers of species and their complex distributions (Hunter *et al.*, 1988) and requires an efficient system for data acquisition and land evaluation. One system is a multi-level approach using the analogy of 'coarse- and fine-filters' to capture maximum biological diversity within conservation reserves (Noss, 1987). The coarse-filter focuses on higher levels of biological organization; the aim is to represent samples of each community in reserves. A representative sample of communities, because of their predictable structure, composition and distribution, is expected to harbour the majority of species. Although the success of this approach would depend on how communities were defined, communities could not be expected to represent all species adequately, especially rare species or populations of more common species with particular significance (Keith and Sanders, 1990). A complementary approach, the fine-filter, uses a classification system designed to capture those species which 'fall through' the coarse-filter (Noss, 1987).

In Australia, classifications of rare plants on national (Briggs and Leigh, 1988) and state-wide scales (Rye and Hopper, 1981; Gullan *et al.*, 1990) provide input for a fine-filter approach. Although these studies focussed on rare species, the conservation significance of populations which are unusual, outlying, geographically important or otherwise of special interest has also been recognized (Leigh *et al.*, 1981). Regional


Nimmitabel
Mumbulla Mtn
Brown Mtn
Bega
Bombala
Pambula
Burragate Peak
Eden
Letts Mtn
Mt Tennyson
Nungatta Mtn
Mt Poole
Mt Imlay
State Forest, Forest Preserve, Flora Reserve & Vacant Crown Land
National Park, Nature Reserve & State Recreation Area
0 5 10 15 20 km

classifications have made some attempt to identify such populations (Forbes *et al.*, 1981; Binns, 1987; Keith and Benson, 1988; Pressey *et al.*, 1990).

The far south coast of New South Wales (Fig. 1) contains large areas of natural vegetation where land-use conflicts have arisen between conservation, timber harvesting and agriculture. A classification of plant communities (Keith and Sanders, 1990) provides a coarse filter for conservation planning and management in the region. This paper provides a complementary fine filter for vascular plant species of conservation significance.

Methods

Significance Categories

Explicit criteria were adopted to classify species of special conservation significance. If the basic goal of conserving all species is to be achieved the categories must identify species whose rarity may allow them to be missed by coarse-filter approaches. Of primary concern are species for which the Eden region contains the major, if not the only opportunities for conservation. These include rare or uncommon species, as well as those common within the Eden region but restricted elsewhere. A regional coarse-filter approach may also miss species which are common outside the region, but uncommon within. Some of the significance categories were designed to address these different levels of rarity. Other categories were designed to identify species at the extremes of their geographical and ecological ranges. Although these species may be conserved elsewhere, their conservation within the region will ensure a more comprehensive representation of their genetic and ecological variability. The categories addressing these areas of conservation significance are described below. They are not mutually exclusive except where stated.

1. **Species endemic to the Eden region**, i.e. not known to occur beyond the study area (Fig. 1).
2. **Rare or threatened Australian plants** are listed on a national register (Briggs and Leigh, 1988) compiled in accordance with guidelines of the International Union for Conservation of Nature and Natural Resources (IUCN, 1980). Species are coded according to the perceived threat to their survival as rare, vulnerable, endangered or extinct and according to the extent of their distributions.
3. **Species uncommon throughout their distribution** have small populations scattered over a broad distribution. Although not considered nationally rare, some are rare or threatened in Victoria (Gullan *et al.*, 1990).
4. **Species restricted outside the Eden region**, regardless of their rarity within. These species are rare or threatened in Victoria, if recorded there at all.
5. **Species uncommon within the Eden region**, but common or widespread beyond.

Fig. 1. Map of the Eden region showing Nature Reserves (1 — Bellbird Ck, 2 — Bermagui, 3 — Bournda, 4 — Egan Peaks, 5 — Goura, 6 — Nadgee), National Parks (7 — Ben Boyd, 8 — Mimosa Rocks, 9 — Mt Imlay, 10 — Nalbaugh, 11 — Nungatta, 12 — Wallaga Lake), a State Recreation Area (13 — Bournda), Flora Reserves (14 — Brown Mountain, 15 — Jingera, 16 — Maxwells Creek, 17 — Narrabarba, 18 — Nethercote, 19 — Nullica, 20 — Nunnock Swamp, 21 — Tennyson Creek, 22 — Waratah Creek, 23 — Watergums Creek, 24 — Werrinook), Forest Preserves (25 — Bondi Gulf, 26 — Coolangubra Escarpment, 27 — Illawambra, 28 — Mt Pericoe, 29 — Mt Poole, 30 — Myrtle Mountain, 31 — Rockton, 32 — Waalimma Montain, 33 — Yambulla), State Forests (34 — Bemboka, 35 — Bermagui, 36 — Bombala, 37 — Bondi, 38 — Broadwater, 39 — Bruces Creek, 40 — Cathcart, 41 — Coolangubra, 42 — East Boyd, 43 — Glen Allen, 44 — Glenbog, 45 — Gnupa, 46 — Mumbulla, 47 — Murrabrine, 48 — Murrah, 49 — Nadgee, 50 — Nalbaugh, 51 — Nullica, 52 — Nungatta, 53 — Tanja, 54 — Tantawangalo, 55 — Timbillica, 56 — Towamba, 57 — Yambulla, 58 — Yurammie), vacant crown land (59 — Bega Swamp, 60 — Coolumbooka, 61 — Murrah, 62 — Pambula River) and freehold land (63 — Bega Valley, 64 — Monaro Tableland, 65 — Towamba Valley).

Some may be rare or threatened in Victoria. Species were not listed in this category if listed in categories 1-4.

6. **Species depleted in the wild** occur in habitats which have been substantially lost, altered or threatened. They are not yet considered nationally rare or threatened, but a considerable proportion of their numbers persist in modified habitats where their long-term conservation cannot be guaranteed.
7. **Species reaching the limit of their geographic distribution in the Eden region**. This includes species which reach the limit of their main distribution in the Eden region, but which have small outlying populations further afield (i.e. local distributional limits).
8. **Species with geographically disjunct populations in the Eden region**.
9. **Ecologically disjunct populations** occupy a habitat atypical for their species.

Data Acquisition

A preliminary list of species satisfying the significance categories was compiled from the site data (0.04ha quadrats) of Keith and Sanders (1990) and floristic lists collated by Binns (1987). These species were further investigated by checking the records of local vegetation surveys (Brechwoldt, 1979; Clarke, 1989; Dodson *et al.*, 1989; Fanning and Mills, 1989; Fanning and Rice, 1989; Garvin, 1982, 1984; Gilmour, 1983), searching the taxonomic literature (*Telopea, Brunonia*, etc.) and searching herbarium records held at the National Herbaria of New South Wales (NSW) and Victoria (MEL), Herbium Australiense (CANB) and the National Botanic Gardens (CBG). The forestry herbarium at Eden (EFC) was not searched directly; however, the records it contains were obtained from other sources (e.g. Binns, 1987; Fanning and Mills, 1989). A list compiled from these sources was circulated for comment to 30 botanists including taxonomic specialists and vegetation surveyors with experience in the Eden region. Their comments yielded extra localities, additional species and deletions. Additional species were investigated in herbaria, survey records and the literature. The conservation status of each of these species in Victoria was checked by consulting Gullan *et al.* (1990).

To reduce subjectivity and maintain consistency in decisions, operational rules were adopted.

i) Species were included on the list only if their presence in the region was substantiated by a specimen lodged in a herbarium or checked by the author. Other records of these species were then included unless shown to be incorrect. This rule excluded some unusual records from species lists which remain unconfirmed or which were shown to be erroneous.

ii) Species were recorded as uncommon within the region if known from four or less localities. This represents a minimal frequency of occurrence in the thirteen hundred quadrat records and species lists available for the region and supplemented by over a century of botanical collections. Comparable, though less conservative selection rules were applied in regional studies of Forbes *et al.* (1981) and Binns (1987). Species with four or less records were not considered regionally uncommon if they were under-represented in survey records and herbarium collections because of their inconspicuous habit or poorly surveyed habitat. This applied to some geophytes and freshwater aquatics. Species with more than four records were considered regionally uncommon if their records were known to represent small populations.

iii) Species were at the limit of their distribution in the Eden region if herbarium collections, the taxonomic literature and survey literature from adjacent regions

(Adams and Craven, 1976; Forbes *et al.*, 1981; Mills, 1989) yielded no records further afield.

iv) Populations were geographically disjunct if the nearest record was over 100km away.

Results

The list of species with special conservation significance is given in the Appendix. Table 1 gives a break-down of species in each category. It is planned to publish details of site records, herbarium specimens, literature searched and botanists' comments. Of over 600 taxa investigated 425 satisfied one or more of the significance categories. About half the 40 nationally rare or threatened species (Category 2) were concentrated in two main areas (Fig. 2): 13 occurred on rhyolite outcrops in the Yowaka River — Narrabarba Hill area, of which 7 are locally endemic; and 8 occur on Nalbaugh Plateau — Wog Wog Mountain, of which one is locally endemic. Dr George Mountain, Mt Imlay, Jingera Rock and Mt Poole also support several rare or threatened species. Three of the 13 endemic taxa (Category 1) are not currently included on the listing of rare or threatened Australian plants (Briggs and Leigh, 1988). A further 7 species have distributions extending just beyond the Eden region (Category 4), including 4 rare or threatened species.

Table 1

Number of species satisfying each selection criterion

Selection criterion	Number of Species
1. Locally endemic	13
2. Rare or threatened in Australia	40
3. Uncommon throughout species distribution	34
— and rare or threatened in Victoria (3v)	(6)
— not rare or threatened in Victoria (3)	(28)
4. Restricted outside the Eden region	7
— and rare or threatened in Victoria (4v)	(2)
— not recorded in Victoria (4)	(5)
5. Uncommon within the Eden region	279
— and rare or threatened in Victoria (5v)	(34)
— not rare or threatened in Victoria (5)	(245)
6. Depleted in the wild	8
7. Limit of geographic distribution (tota)	183
— northern limit (7N)	(38)
— southern limit (7S)	(137)
— local northern limit (7LN)	(5)
— local southern limit (7LS)	(3)
8. Geographically disjunct population	23
9. Ecologically disjunct population	8

Note: Criteria are not mutually exclusive. Numbers in parentheses are subtotals within categories. Significance codes are those used in the Appendix.

Thirty-four species were classified as uncommon throughout their distribution (Category 3), including 6 regarded as rare or threatened in Victoria. Category 5 was the largest with 279 regionally uncommon taxa, of which 34 were listed as rare or threatened in Victoria (Gullan *et al.*, 1990). About two-thirds of these were not listed under any other category, including a number of subalpine species at the lower end of their altitudinal range. Most of the remainder were at the edge of their distribution (Category 7). Regionally uncommon taxa were concentrated in heath and woodlands of

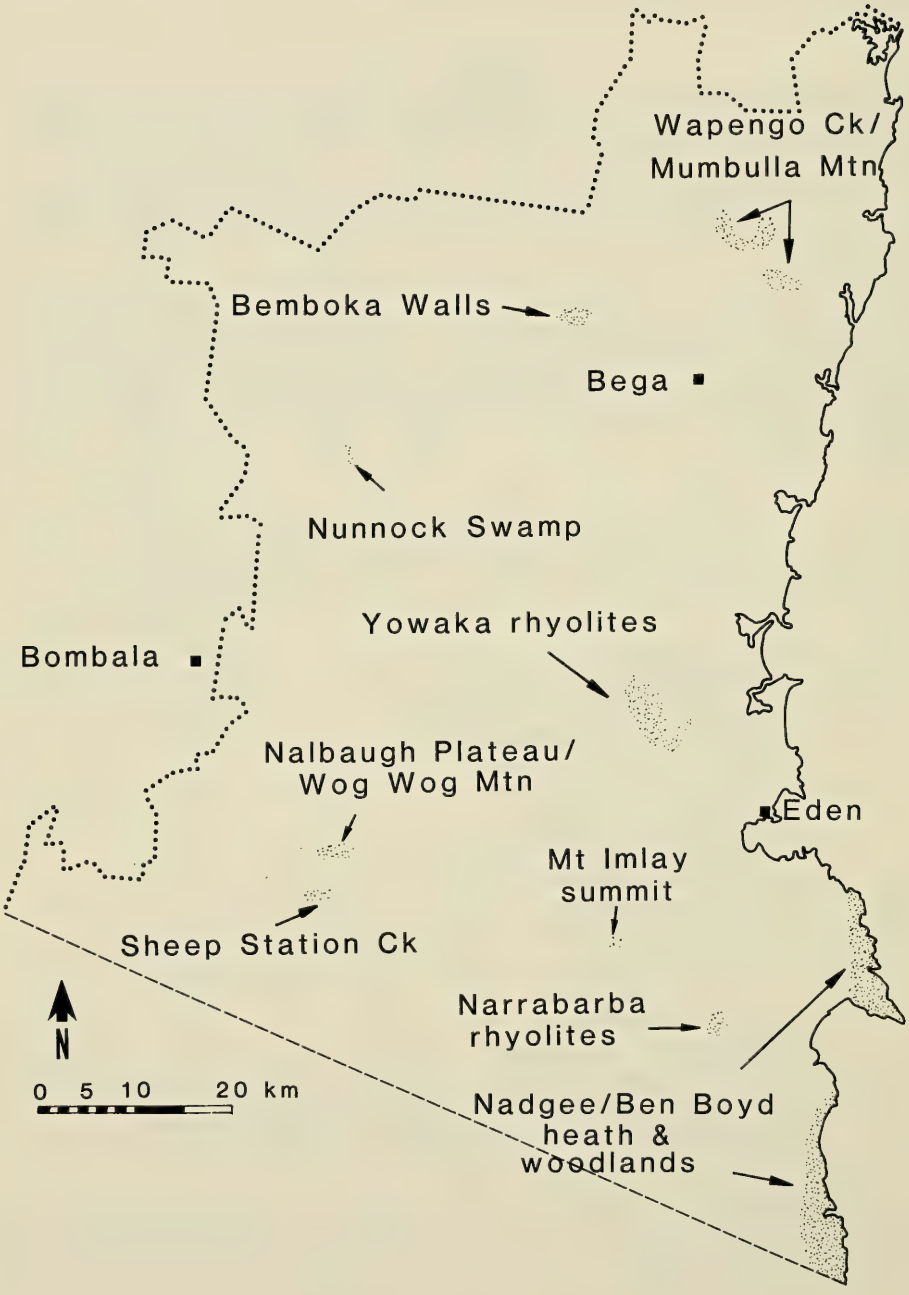


Fig. 2. Map showing concentrations of rare and biogeographically significant plant species.

Nadgee Nature Reserve and Ben Boyd National Park, Nunnock Swamp, along Sheep Station Creek and on rhyolite outcrops (Fig. 2).

Rabinowitz (1981) proposed a typology of rare species based on geographic range, habitat specificity and local population size which may be applied to rare or uncommon taxa in categories 1-4 (Table 2). Most of the endemic rhyolite flora and several mountain endemics are sparse, geographically restricted and limited to specific habitats. Some geographically restricted species attain relatively large populations, while some with specific habitats extend over quite large geographic ranges. However, there were relatively few species with small geographic ranges and broad habitat specificity. *Myoporum bateae*, ranging from the tableland escarpment to the coast, and *Persoonia brevifolia*, spanning several hundred metres in elevation, may be examples with relatively large and small local populations, respectively. Rabinowitz (1981) made a similar observation amongst rare flora in North America, suggesting demographic stochasticity as a mechanism by which habitat specificity may be narrowed, pushing such species to the right of Table 2. Alternatively, they may be pushed to the left of Table 2 if their rate of dispersal to like habitats is greater than the rate of genetic diversification allowing establishment in new habitats.

TABLE 2

Examples of different types of rarity (after Rabinowitz, 1981)

Geographic Range:	**Large**		**Small**	
Habitat Specificity:	Wide	Narrow	Wide	Narrow
Local Population Size				
Large	Common species	*Burnettia cuneata* *Boronia deanei* *Eucryphia moorei*	*Myoporum bateae* *Acacia georgensis*	*Acaacia constablei* *Daviesia suaveolens* *Eucalyptus badjensis*
Small	*Cryptostylis hunteriana*	*Botrychium australe*	*Persoonia brevifolia*	*Phebalium ralstonii*
	Hovea beckleri	*Phebalium carruthersii*	*Pomaderris brogoensis*	*Eucalyptus imlayensis*
	Pseudanthus divaricatissimus	*Mitrasacme serpyllifolia*		*Caladenia* sp. aff. *fitzgeraldii*

Of the eight species depleted in the wild (Category 6), five were trees or herbs whose habitat has been extensively modified by agricultural clearing and three were epiphytic orchids potentially threatened by collectors. Since agricultural areas have been poorly surveyed, there are undoubtably more species whose populations have been substantially depleted.

One hundred and eighty-three species reached their known limit of distribution in the Eden region (Category 7). The majority of these (137) reached their southern limit, including a number of rainforest taxa in the forests north of Bega and sclerophyll shrubs in heath and woodland south of Eden. Most of the 38 taxa reaching their northern limit occur in the southern part of the study area. Some of these species (e.g. *Diuris corymbosa, Pomaderris elachophylla*) could equally be interpreted as reaching eastern limits since their distributions are trans-temperate.

The excess of species reaching southern limit over those reaching northern limit illustrates a latitudinal trend in vegetation of south-eastern Australia (Keith and Sanders, 1990). The species listed show that the sclerophyll flora as well as the rainforest flora (Webb *et al.*, 1984) becomes impoverished with increasing latitude.

Twenty-three species are represented in the Eden region by geographically disjunct

populations (Category 8). These occurred mainly on rhyolite outcrops around Yowaka River and on mountain peaks including Mt Imlay and Nalbaugh Plateau. Eight species have ecologically disjunct populations including three coastal occurrences of predominantly inland species, two non-coastal occurrences of littoral species, one low altitude occurrence of a tableland species, one montane occurrence of a coastal species and one species on an uncharacteristic soil type.

Discussion

The typology of Rabinowitz (1981) offers some guidelines for conservation and management of rare species. The size of geographic range will influence the cost of conserving rare species. Although there may be more opportunities for reserving species with broad geographic ranges, more reserves would be required to represent these species thoughout their range compared with those with more restricted geographic occurrence. Habitat specificity has an important influence on the cost effectiveness of biological surveys. Species with narrow habitats could be searched for more efficiently than those with broader, less predictable habitats. Special purpose surveys for species with narrow habitats would therefore be profitable. For species with broad habitats, survey effort might be better directed into general purpose surveys which cover a broad range of environments. Such decisions pre-suppose the existence of sufficient data to determine (at least in rough terms) the habitat specificity of the species involved.

The sizes of local populations also have implications for the management of rare species. An understanding of population dynamics and the role of disturbance may be most critical for species with small populations, since small fluctuations may lead to local extinctions. On the other hand, large populations may fluctuate widely, depending on the life cycle attributes of the species. There have been mechanisms demonstrated by which large populations may be driven to extinction in a very short period of time (Noble and Slatyer, 1980). Further complications to the study of rare species characterized by small populations include the difficulty of obtaining adequate replication and the concern that manipulative experiments (which often provide the best understanding of ecological responses) may cause significant reductions in species' numbers.

Changes in rarity through time (Harper, 1981) were not examined in this study. However, it may be assumed that species with limited geographic ranges and specific edaphic habitats, such as rocky rhyolite outcrops, have probably always been so, even though their local abundance may vary in response to disturbances such as fire. However, the availability of some currently restricted habitats may change in response to climatic fluctuations. For example, rare species of swamps (e.g *Boronia deanei*) and rainforests (e.g. *Eucryphia moorei*) may have been both more locally abundant and more geographically widespread in wetter times.

The large number of regionally uncommon species is a consequence of the log-normal species-abundance distribution of the regional flora (Fig. 3). Three hundred and thirty-eight species (44% of total) were recorded in less than 4 of 369 quadrats (i.e. <1%) in the survey of Keith and Sanders (1990). Over 200 additional species known to occur in the region were not sampled in any quadrats. Margules and Usher (1981) point out that sample data from many different groups of organisms conform to this model, a recent example being the abundance distribution of rare species in the flora of the southern Appalachians (Miller and Wiegert, 1989). Thus, any reasonably large regional biota could be expected to contain a large proportion of uncommon species.

The large number of species listed and their relatively even distribution throughout the study area have implications for the cost of their conservation. Clearly, not all categories are of equal priority for conservation. Locally endemic and nationally rare or

threatened species must receive the highest priority since opportunities for their conservation are most limited. Species listed only as regionally uncommon (Category 5) are perhaps the lowest priority since they may be expected to be conserved by coarse-filter approaches in other regions.

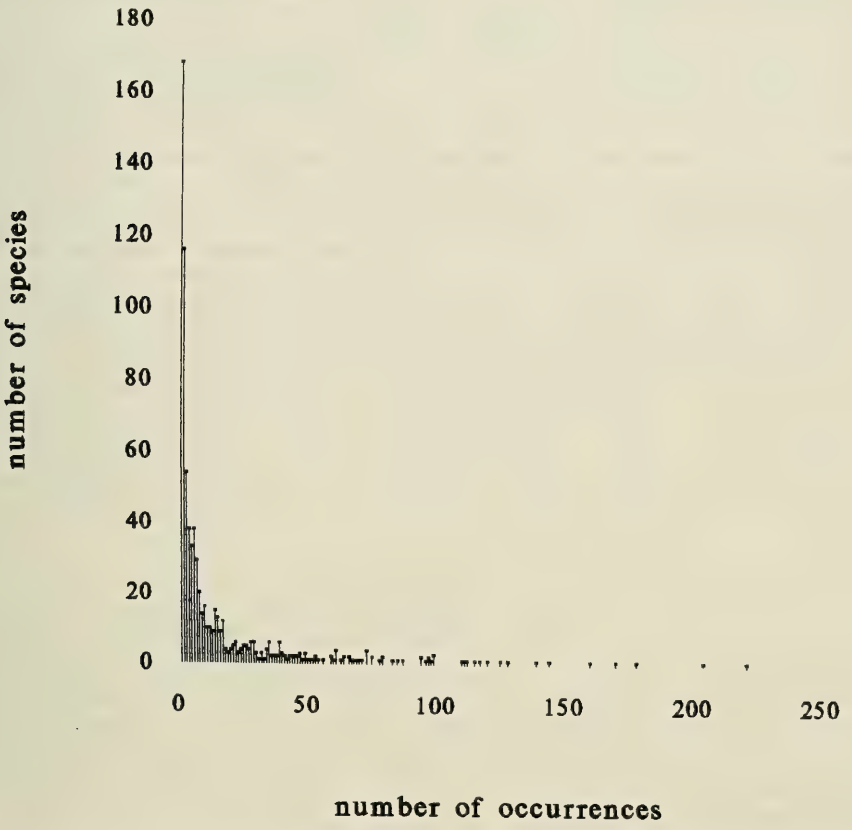


Fig. 3. Species-abundance distribution showing a large number of uncommon species (i.e. occurring in a small number of quadrats) and a small number of common species in the Eden regional flora. Data from Keith and Sanders (1990).

Nevertheless, there are strong arguments for conserving representative samples of species throughout their geographic and ecological ranges. Geographic and ecological variation in gene pools has been demonstrated within a wide range of species throughout the world (Heslop-Harrison, 1964; Brown, 1978; Hamerick, 1983; Moran and Hopper, 1983; Bramwells and Whiffin, 1984; Mackay and Morrison, 1989). Further, the same species may perform different ecosystem roles in different geographic locations where its interactions may involve different competitors, predators and pathogens. Reservation of narrow samples of species' distributions therefore may not represent their full genetic diversity, nor the full range of ecological processes in which they are involved. Representation would be improved by inclusion of outlying populations and those at the extremes of species' distributions. Such populations may yield important data for research in the fields of autecology, biogeography and bioclimatic history. Species depleted in the wild also warrant attention because even though they may

presently be common on farmland or wasteland, seedling recruitment may be limited by grazing, soil compaction, weeds, etc. Stands of natural vegetation containing these species are therefore valuable for long term conservation as well as for ecological studies of natural patterns and processes.

A fine-filter approach to conservation planning using the significance categories applied in this study would clearly result in a more representative reserve system than one which includes only the rarest species. However, there is an obvious trade-off between representativeness and cost. Work is in progress to find the most efficient solution to this problem by identifying a minimum set of areas which contain a fully representative complement of the region's biota. The role of the fine-filter in this work is to identify areas where poorly represented species of conservation significance are concentrated. The Yowaka area is outstanding in this regard.

The listing is constrained by the availability of data which, although substantially increased in recent years, are relatively modest compared to those available for East Gippsland to the south. With more data, the listing will undoubtedly change and updated versions will be published in due course. Perhaps most changes will occur in the regionally uncommon category as unsubstantiated records of many species are verified in future by herbarium specimens, while others are shown to be more common. Although decisions to include or exclude species from the listing involve some subjectivity, I have tried to minimize this by using explicit significance categories and operational rules, and by testing the classification with the opinions of other botanists. Criteria 6 and 9 have been applied very conservatively. A greater understanding of ecological relations may indicate more species are worthy of these classifications.

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APPENDIX

List of rare and biogeographically significant vascular plant species in the Eden Region

Numbers in parentheses refer to areas of land shown in Fig. 1. Where a locality spans two or more such areas, their numbers are separated by a comma. Where the record of a locality is imprecise and could belong to two or more areas, their numbers are separated by a slash. Question marks indicate the precise locality of the record is uncertain. Where a significance category is marked by an asterisk, this refers only to the locality marked with an asterisk. If the locality of a distributional limit is from an old or imprecise record, the nearest precise locality is given in square brackets. Place names are shown on 1:25,000 topographic maps (NSW

roads or watercourses indicate the locality is at their intersection. Where place names are separated by a dash, the locality is between these places.

Abbreviations: Ck — Creek; Mtn — Mountain; Stn — Station; Rd — Road; Hwy — Highway; N — North; S — South; E — East; W — West.

Categories of Significance

1. Endemic to Eden region
2. Rare or threatened in Australia, codes of Briggs and Leigh (1988) given in parentheses
3. Uncommon throughout species distribution, not rare or threatened in Victoria
3v. Uncommon throughout species distribution and rare or threatened in Victoria
4. Restricted outside the Eden region, not recorded in Victoria
4v. Restricted outside the Eden region and rare or threatened in Victoria
5. Uncommon within the Eden region, not rare or threatened in Victoria
5v. Uncommon within the Eden region and rare or threatened in Victoria
6. Depleted in the wild
7N. Northern limit of geographic distribution
7S. Southern limit of geographic distribution
7LN. Local northern limit of geographic distribution
7LS. Local southern limit of geographic distribution
8. Geographically disjunct population
9. Ecologically disjunct population (atypical habitat)

Species	Significance	Localities
Acacia aculeatissima	7N	Bimmil area (51)
Acacia constablei	1,2(2V)	Narrabarba Hill & nearby ridges (17)
Acacia costiniana	2(3RCa),7S,8	Nalbaugh Plateau (10)
Acacia elongata	7S	White Rock River (37)
Acacia georgensis	1,2(2VCi)	Dr George Mtn (8,53), Kianniny Bay (13)
Acacia gunnii	5	Sheep Station Ck (31), White Rock River (37), Laings Rd (37), western Bondi (37), Wallagaraugh River/Yambulla Trail (57)
Acacia irrorata sp. *irrorata*	5v	Bermagui (1), Dignams Ck-Wallaga Lake (5,12), Wog Wog Rd (37), Cuttagee Ck (48), Quaama (63)
Acacia lanigera	5	White Rock River (37), Wallagaraugh River/Imlay Ck (57)
Acacia maidenii	5v	1km N Grassy Hill (5), Bunga Head (8), Picnic Pt (8), Dignams Hill-Wallaga Lake (12), 2.2km ESE Big Jack trig (65)
Acacia mucronata	7N	Tantawangalo lookout (54), near Rats Valley Rd/Chalkhills Rd
Acacia oxycedrus	5,7LN*	Mt Nadgee (6,49)*, Mt Victoria (6), W of Impressa Moor (6)
Acacia pycnantha	5,9	Nelson Lagoon (8), Mumbulla (46), Cuttagee Ck (48), Black Fellows Lagoon (63) — coastal localities
Acacia rubida	5	Jingera Rock (4), Genoa River (11), 16km N Timbillica (55), Quaama (63), Bermagui
Acacia silvestris	5,7LS*	Mumbulla Mtn (46), Brogo Pass (61), Wolumla Peak (58)*, Quaama (63)
Acacia subporosa	4v,7N*	Sandy Beach Ck catchment (3), Jellat Jellat Ck catchment (3), S gullies of Black Range (3), head of Wirra Birra Ck (6), Disaster Bay (6), Tumbledown Mtn (6), Tabletop Mtn (6), Mt Victoria (6), Nadgee River flats (6), Wapengo Lagoon (8), Bengunnu Pt (8), 1.5km W Tathra Rd/Neilsen Rd (8), Aragunnu Ck (8)*, Nethercote Falls (18), Mt Nahgi (49), Bimmil area (51), Palestine Ck (51), Yellow Pinch (58), 5km N of Pambula, Pambula-Eden, Quarantine Bay
Acacia subtilinervis	2(3RCa)	Nethercote Falls (18), Yowaka-Old Hut rhyolite outcrops (15,47,51), Bemboka Walls (34)
Acacia vestita	5	Imlay Rd (57), Candelo (63), 'Colombo' (63)
Acaena ovina	5	Big Jack Mtn (41), Mt Pericoe (28), Pooles Gully (57)
Acianthus fornicatus	7S	Rhyolite ridge S of Narrabarba (17)
Acrotriche leucocarpa	3	Wog Wog Mtn (10), 0.5km SSW White Rock Mtn (10), Compartment 1328 (41), Pheasants Peak (41), Wattle Rd (46), Nalbaugh (50)

APPENDIX (Cont'd.)

Species	Significance	Localities
Actinotus gibsonii	3,7S,8	Heath near Bombala (?37,41,60)
Actinotus helianthi	5,7S*	Mt Imlay summit (9)*, Tura Beach (13)
Adriana glabrata	5	'Willeroo' (65)
Aegiceras corniculata	7S	Merimbula
Agrostis sp. *'hiemalis'*	5	Dragon Swamp (20), Nitens Rd (46)
Alectryon subcinereus	5v	S gullies of Black Range (3), Bunga Head (8), Wapengo Ck (46), Rocky Hall (41,65), Yellow Pinch (58), Bega River (63)
Allocasuarina diminuta ssp. annectens	5,7S,8	Wallagaraugh River/Imlay Ck (57)
Allocasuarina distyla	5,7S*	Green Cape (7)*, Nelson Lagoon (8), upper Genoa River (?37)*
Ammobium alatum	5	Bega (63), Cobargo (63), Nungatta Stn
Amphipogon strictus	5	Tumbledown Mtn (6), Sheep Station Ck (31)
Amyema congener	5,7S*	Bega area (63), 'The Breakaway'-Bermagui, Merimbula*
Apalochlamys spectabilis	3,7N*	Cape Howe (6), Yambulla catchments (57)*
Aphanopetalum resinosum	7S	Wally Newtons Inlet (6), Watergums Ck (23)
Aristida vagans	7S	Upper Sheep Station Ck (31)
Arthropteris tenella	5,7S*	Bunga Head (8), Broadwater (38)*
Asplenium australasicum	5,7S	Bunga head (8), Murrah River tributary (61)
Asterolasia asteriscophora	5	Genoa River gorge (11)
Astroloma pinifolium	5	Nelson Beach (?8/63), S end Gallery Rd (55) experimental plot (57)
Astrotricha asperifolia	5	Northern Yambulla (57)
Astrotricha sp. aff. *longifolia*	5	Mt Victoria (6), Watergums Ck (23)
Atherosperma moschatum	5	Nalbaugh Plateau (10), Brown Mtn (14), Brown Mtn Ck (24), western Bondi (37), Compartment 2304 (46)
Backhousia myrtifolia	7S	Wapengo Ck (46)
Baeckea denticulata	2(3RCa),7S	Coolumbooka Range (41,60)
Baeckea ramosissima ssp. *prostrata*	5	Impressa Moor (6), 2km N Little River (6), Saltwater Ck (7), near Green Cape (7)
Banksia paludosa	7S	Nadgee Lake (6)
Banksia spinulosa var. *cunninghamii*	7LN	Mt Imlay summit (9), Green Cape Rd (42)
Banksia spinulosa var. *spinulosa*	7S	Broadaxe Rd/Bingera Rd (57)
Beyeria viscosa	5v	Wog Wog Mtn (10), Neenah Gorge (11)
Blechnum chambersii	5	Nadgee (6), Neenah Gorge (11), Nungatta homestead
Boronia deanei	2(3VCa),7S,8	Nalbaugh Swamp (10)
Boronia nana var. *hyssopifolia*	5	Nunnock Swamp (20), Bondi Gulf (25)
Boronia polygalifolia	5	Pambula River (62)
Boronia rigens	5,7S	Yowaka-Old Hut Ck rhyolite outcrops (47), hill E of Bombala (64)
Botrychium australe	3v	Sheep Station Ck (31)
Brachyscome cardiocarpa	5	Surveyors Gully (11), Nunnock Swamp (20), Dragon Swamp (20), Waratah Ck (22)
Brachyscome scapigera	5	Head of Reedy Ck (41), Knox Valley (?54), Yambulla Flat (57)
Breynia oblongifolia	7S	Nadgee (6)
Brunoniella pumilio	5v	Nelson Lagoon (8), Goats Knob Rd/Neilsen Rd (8)
Burnettia cuneata	2(3RC-),8	Top Moor (6)
Caladenia congesta	5	Nadgee area (6), Nungatta (11), Yambulla (57)
Caladenia deformis	5	Nadgee area (?6/49), headland S of Woodburn Ck (7)
Caladenia tesselata	2(3V)	Genoa River (?11/25/37)
Caladenia sp. aff. *fitzgeraldii*	3,7N	3km W Wonboyn (49)
Callitriche muelleri	5	Maxwells Ck (16)
Callitris muelleri	5,7S	Eden district

APPENDIX (Cont'd.)

Species	Significance	Localities
Calotis glandulosa	2(3VC-),7S	Mt Imlay (9), nth Rockton section (37)
Cardamine lilacina	5	Reedy Ck (41), E of Bombala
Carex declinata	5,7S*	Letts Mtn (57)*, 11 km WNW Cobargo (?47/63)
Carex fascicularis	5	Sheep Station Ck (31), Narrabarba Ck/Wonboyn Rd (42/49)
Carex polyantha	5	Taskers Flat (37), Tantawangalo Ck (46), Smiths Rd/Lizard Rd (46), Murrah River tributary (61)
Cassia odorata	5,7S	Near Dr George Mtn (8), Tanja
Cassinia aureonitens	5,7S,8	Nethercote Falls (18)
Cassinia cunninghamii	5,7S,8	Bermagui-Eden area near coast
Cassinia uncata	5	Merrica River crossing (6), sth Ben Boyd (7)
Casuarina cunninghamiana ssp. *cunninghamiana*	5,7S*	1km SE Boundary Bridge (5), Narira Ck (12), Murrah River tributary (61)*, Brogo River (63)*
Casuarina glauca	5,7S	Wallaga Lake (12)
Caustis recurvata	5,7S	Merrica River Rd (49), Yambulla catchments (57)
Celastrus subspicatus	5,7S,8	2km W Mogarika Inlet (63)
Celmisia longifolia	5	Bega Swamp (59)
Centipeda minima	5	Nadgee (6), Sheep Station Ck (31), Big Jack Mtn (41), Walla Walla trail (57)
Cheilanthes distans	5	Mt Pericoe (28), Yowaka-Old Hut rhyolite outcrops (51)
Choretrum candollei	7S	Falkner Ck/Indigo Ck (57)
Chorizema parvifolium	3,6,7S	Bega area (63)
Cissus antarctica	5,7S	Ganes Bay (13)
Citriobatus pauciflorus	7S	Wapengo Ck (46)
Claoxylon australe	7S	Rocky Hall trail (41)
Clematis microphylla var. *leptophylla*	5	2.5km NW Burragate Peak (4), Lake Nadgee Beach (6), Cape Howe (6)
Comesperma retusum	5	Nunnock Swamp (20), Sidlings Swamp (55)
Comesperma sphaerocarpum	5,7S	Wonboyn Rd (?42/49)
Correa baeuerlenii	2(2VCi),7S*,8	Bunga Head (8), 1km E Mumbulla Mtn (46), Wapengo Ck (46)*, Murrah River tributary (61)
Cotula alpina	5	Dragon Swamp (20), Tantawangalo Mtns (54)
Craspedia sp. 'L'	5	Nunnock Swamp (20)
Cryptandra amara var. *longiflora*	5	Narrabarba Hill (17), Imlay Ck/Imlay Rd (57), Yambulla catchments (57)
Cryptandra ericoides	5v	Impressa or Nadgee Moor (6), Green Cape (7), Bingera Rd area? (57)
Cryptandra scortechinii	5,7S	Bermagui
Cryptostylis hunteriana	2(3VC-)	Nadgee (6), Mowarry Track (7), Nethercote Falls (18)
Cyathea leichhardtiana	5v	Head of Nadgee River (6), heads of Royds & Maxwells Cks (16), Watergums Ck (23)
Cyathea marcescens	3v,7N	Head of Maxwells Ck (16)
Cymbidium suave	7S	Goats Knob Rd/Neilsen Rd (8)
Cyperus gunnii	5	Kiah River (65), Wallaga Lake, Boydtown Rd, Narrabarba
Cyperus lhotskanus	5	Eden-Pambula
Cyperus sanguinolentus	5	Nadgee (6), Nethercote Falls (18), Mumbulla (46), Boydtown
Danthonia eriantha	5	Nunnock Swamp (20)
Danthonia setacea	5	Impressa Moor (6), Wally Newtons Inlet (6), Sidlings Swamp (55), Middle Head-Eden
Davallia pyxidata	5,7LS*	Bemboka Walls (34), Yowaka-Old Hut rhyolite outcrops (51)*
Daviesia acicularis	5,7S*	4km W Saltwater Ck (7)*, Yowaka-Old Hut rhyolite outcrops (51)
Daviesia alata	5,7S*	Near Green Cape (7), near Narrabarba (42)*
Daviesia corymbosa	5,7S*	Green Cape (7)*, nth Rockton section (37), East Boyd -E of Hwy (42)*, 1.4km W Tathra (63)
Daviesia suaveolens	2(3RCa),7S	Pigeon Box Mtn (34), Mistake Trail (34)
Daviesia wyattiana	5v	Yowaka-Old Hut rhyolite outcrops (51), Twofold Bay
Dendrobium aemulum	5,7S.	Tanja (53)
Dendrobium pugioniforme	5,7S*	Mumbulla Mtn (?46/61)*, Wandella Ck (47), Walls Flat (63)

APPENDIX (Cont'd.)

Species	Significance	Localities
Dendrocnide excelsa	5,7S*	400m N Grassy Hill (5), Mumbulla Ck (46)*, Wandella Ck (47), Murrah River tributary (61)
Desmodium brachypodum	5v	Quaama-Brogo Pass (63)
Deyeuxia accedens	2(3RC-),7N*	Nalbaugh Plateau (10), Brown Mtn (14)*, Mt Tennyson (21)
Deyeuxia crassiuscula	5	Wog Wog Mtn (10), Wicks Weir Rd (44), Solomons Rd (46)
Deyeuxia parviseta	5	Brown Mtn (14), Yuglamah Rd (40), Waalimma Range (57), Walla Walla trail (57)
Dillwynia juniperina	5	Waratah gully (22), Nalbaugh (50)
Dillwynia prostrata	5v	Nunnock Swamp (20)
Disphyma australe	5	Jane Spiers Beach (6), Green Cape (7), Bermagui, Merimbula
Diuris corymbosa	5,7N*	Green Glades (6), 1 km W Wonboyn (49)*, Timbillica (?55/57), Yambulla catchments (57)
Dodonaea multijuga	5,7S*,8	Bemboka Walls (34), Yowaka-Old Hut rhyolite outcrops (47,51)*
Dodonaea rhombifolia	2(3RCa)	Jingera Rock (4), Bemboka Walls (34)
Dodonaea triangularis	5,7S	Mumbulla Mtn (46)
Doryphora sassafras	7S	Head of Chalkhills Ck (58)
Drosera glanduligera	5	Twofold Bay
Ehretia acuminata	5,7S*	Grassy Hill (5), Mumbulla Mtn (46), 7.5km W Merimbula (58)*
Epacris breviflora	5	Nunnock Swamp (20), Dragon Swamp (20), Cairnlea (37), Bega Swamp (59)
Epacris microphylla var. *rhombifolia*	3,7S*	Nunnock Swamp (20), Bega Swamp (59)
Epacris robusta	5,7S*	Burragate Peak (4), Jingera Rock (4), Nalbaugh Plateau (10)*, Big Jack Mtn (41)
Epilobium gunnianum	5	Dragon Swamp (20), Sheep Station Ck (31) Nungatta area
Epilobium pallidiflorum	3v,6	Sheep Station Ck (31), Bega (63)
Eriostemon myoporoides	5	Nethercote Falls (18), Bemboka Walls (34), Yowaka-Old Hut rhyolite outcrops (51), Murrah (61)
Eriostemon virgatus	5,7N*,8	Mt Imlay summit (9), 1 km N Burrawang picnic area (?9/42), Yowaka-Old Hut rhyolite outcrops (51)
Eucalyptus badjensis	2(2RCi),7S*	Brown Mtn (14), 4km ESE Bull Mtn (46), Wicks End catchment (44), Wilbob catchment (44), Mt Darragh (?40/54/64)*, New Line Rd (54)
Eucalyptus baueriana	6	W slopes of Black Range (3), Sandy Beach Ck-Jellat Jellat Ck (3), Narira Ck (12), Gnupa (45), Wapengo Ck (46), Bimmil area (51), 3.2 km N Burragate (51), end Waalimma Rd (57), Yurramie (58). Remnant stands in 63, 65 & near Pambula
Eucalyptus baxteri	7N	The Pinnacles (7)
Eucalyptus imlayensis	1,2(2VCit)	Mt Imlay summit (8)
Eucalyptus latiuscula	3,7S*	Nalbaugh Swamp (10)*, Nunnock Swamp (20)
Eucalyptus longifolia	7S	Newtons Beach (6)
Eucalyptus mackintii	5,7N*	Genoa Gorge (11), Saddle Flaps Rd (37)*
Eucalyptus macrorhyncha	5	Cathcart (?64)
Eucalyptus maculata	7LS	Near Yellow Pinch (58) [Neilsen Rd (8)]
Eucalyptus maidenii	9	Dobbyns Rd on basalt (51)
Eucalyptus melliodora	5,9	Upper Towamba valley (65) -a coastal occurrence
Eucalyptus paniculata ssp. *paniculata*	5,7S*	Near Nelson Lagoon (8)*, 3km N Nelson Ck/Tathra Rd (8), Bermagui (35)
Eucalyptus parvifolia	2(2VCi),7S	Dragon Swamp (20)
Eucalyptus pilularis	7S	Nadgee (6), [near Bellbird gully (7)]
Eucalyptus pseudoglobulus	5,7N	Nadgee River (6)
Eucalyptus rubida	5	Waratah Ck (22), Bondi Gulf (25), Coolunbooka (60), 3km W Mt Darragh (64)

APPENDIX (Cont'd.)

Species	Significance	Localities
Eucalyptus stellulata	5	Nunnock Swamp (20), Waratah Ck (22), Cairnlea (37), Collumbooka (60), 5km from Nimmitabel towards Bombala (64)
Eucalyptus stenostoma	5,7S	Near Pigeon Box (34)
Eucalyptus tereticornis	6	Kianinny Bay (13), Merimbula Beach. Remnant stands in Bega valley (63) & near Pambula
Eucalyptus ignorabilis	3,7N*	Merrica River (6), Bens Ck (55), Dinner Ck (55), near Timbillica Stn (57), Imlay Ck/Wallagaruagh River (57)*, Allan Brook crossing (57)
Eucalyptus conspicua	3,7N*	Duck Hole Rd (7), 4km S of Narrabarba (49), Sidlings Swamp (55), 3km N of Wallagaraugh River on Hwy (55), near Timbillica (57)
Eucalyptus sp. aff. *globoidea*	3,7N	Newtons Beach (6)
Eucalyptus polyanthemos ssp. *vestita*	7N	Rocky Hall trail (41), Bruin Mtn (41)
Eucalyptus croajingalensis	7S	Near Nunnock Swamp (20), Packers Swamp (44)
Eucalyptus spectatrix	1	Bemboka Walls (34), Mumbulla Mtn (46), hill N of Mumbulla Mtn (61), Dr George Mtn
Eucryphia moorei	3v	SE of Burragate Peak (4), upper Table Ck (6), upper Nadgee River (6), Maxwells Ck (16), Royds Ck (16), Watergums Ck (23), Wandella Ck (27), Mumbulla (46), Back Ck Trail (51), SW Yambulla (57)
Euphrasia collina ssp. *collina*	7N	Twofold Bay, [Saltwater Ck (7), East Boyd -E of Hwy (42)]
Festuca asperula	3	Tantawangalo Mtn (54), Letts Mtn (57)
Festuca eriopoda	5v	Brown Mtn (14), Six Mile Ck (54)
Festuca hookeriana	5	Brown Mtn (14), Dragon Swamp (20)
Ficus rubiginosa	7S	Mt Pericoe (28)
Gahnia aspera	5,7S*	Bunga Head-Aragunnu Ck (8), Yellow Pinch (58)*, Murrah River tributary (61)
Gahnia subaequiglumis	5v	Mt Imlay summit (9), Nunnock Swamp (20), Coolumbooka (60)
Gaultheria appressa	5	Mt Imlay (9), Nalbaugh Plateau (10), Nungatta Mtn (11), Nalbaugh (50)
Gentianella diemensis	5	Nalbaugh Swamp (10), Dragon Swamp (20), Nunnock Swamp (20), Bega Swamp (59)
Geranium antrorsum	5	Near Nunnock Swamp (20), Big Jack Mtn (41), Bega Swamp (59)
Geranium retrorsum	5	Bega area (?63)
Gleichenia rupestris	5,7S*	Nadgee (6)*, Green Cape (7)
Goodenia elongata	7N	Head of Reedy Ck (41)
Goodenia hederacea var. *alpestris*	5	Nunnock Swamp (20), Tantawangalo Mtn (54), Coolumbooka (60)
Goodenia hederacea var. *hederacea*	5,7S	Head of Cuttagee (48)
Goodenia humilis	5	Green Cape (7), Sheep Station Ck (31)
Goodenia paniculata	5	Cape Howe (6), Allan Brook crossing (57)
Grevillea acanthifolia ssp. *paludosa*	1	Nalbaugh Swamps (10)
Grevillea miqueliana	5	Yowaka-Old Hut rhyolite outcrops (51)
Grevillea mucronulata	5,7S*,8	3km N Merimbula (?3), Mimosa Rocks (8), Hwy S of Eden*
Grevillea parviflora	5	White Rock River (37), Nullica (51), Indigo Ck crossing (57), Wallagaraugh River (57)
Haemodorum planifolium	5,7S	Near Bellbird trig (7)
Hakea macraeana	7S	Adjacent to Nadgee Moor (6)
Hakea ulicina	7N	Green Cape (7), East Boyd (42)
Haloragis heterophylla	5	Dragon Swamp (20), Sheep Station Ck (31), Coolumbooka (60)

APPENDIX (Cont'd.)

Species	Significance	Localities
Haloragodendron baeuerlenii	2(3RCa)	Big Jack Mtn (41), Mumbulla Mtn (46), Brogo Pass (63), Dr George Mtn
Haloragodendron monospermum	3,7S	Coolumbooka Range (60)
Helichrysum acuminatum	5	Nalbaugh Swamp (10), Nunnock Swamp (20), Dragon Swamp (20), Bega Swamp (59)
Helichrysum apiculatum	5	Nadgee (6), 9km E Cathcart (64), McLaughlin River (64), Dr George Mtn
Helichrysum baxteri	7N	Bimmil area (51)
Helichrysum collinum	5,7S,8	2km WNW Murrah River/Mumbulla Ck (61)
Helichrysum conditum	5	Head of Neenah Ck (11), 3km SW Nungatta trig (11)
Helichrysum diosmifolium	7S	Yambulla catchments (57)
Helichrysum obtusifolium	7N	Saltwater Ck (7)
Helichrysum paralium	7N	3.5km SE Tanja (8)
Helichrysum rosmarinifolium	5,7LN*	Nalbaugh Swamp (10)*, Sheep Station Ck (31), western Bondi (37), Sidlings Swamp (55)
Helichrysum thyrsoideum	5	Nungatta (11), Cairnlea (37)
Hibbertia hermanniifolia	2(3RCa)	Mt Cathcart & surrounds (40), Tantawangalo (54), Mt Poole (57)
Hibbertia saligna	3,7S,8	Mt Imlay summit (9)
Hibbertia serpyllifolia	5	Impressa Moor (6), Pinnacles (7), Yambulla (57)
Hibbertia sp. aff. *hermanniifolia*	1	Yowaka-Old Hut rhyolite outcrops (51) (taxonomic status to be determined)
Hovea beckeri	3	Wog Wog Mtn (10), Bondi Gulf (25), Myanba Ck (41), Indigo Ck crossing (57)
Hovea longifolia	5,7S,8	Waalimma Range (57)
Hybanthus monopetalus	5	S of Kianniny Bay (13), Mumbulla (46), Dr George Mtn
Hydrocotyle algida	5	Dragon Swamp (20)
Isachne globosa	3	Sheep Station Ck (31), Link Rd (49), Bega area (?63)
Isolepis aucklandica	5	Nadgee Lake (6), Dragon Swamp (20)
Isolepis crassiuscula	5	Brown Mtn (14)
Isopogon prostratus	3v	Newtons Beach (6), Nadgee Moor (6), Green Cape (7), Nethercote Falls (18), White Rock River (37), Mt Nadgee (49)
Isotoma fluviatilis ssp. *australis*	5	Sth Ben Boyd (7), Nunnock Swamp (20), Coolumbooka (60)
Juncus falcatus	5	Dragon Swamp (20), Bega Swamp (59), Coolumbooka (60)
Juncus fockei	5	Sheep Station Ck (31), head of Reedy Ck (41), Bens Rd (55)
Juncus homalocaulis	5	Lower Nungatta Ck (11), Hopping Joe Ck (37)
Juncus vaginatus	5	Nadgee (6), Bega Swamp (59)
Juncus sp. F ('*phaeanthus*' ms)	5	Dragon Swamp (20)
Juncus sp. (aff. *sandwithii*)	5	Western Bondi (37)
Korthalsella rubra	3v	Watergums Ck (49), 1 km SE Ben Boyd Rd/Dobbyns Rd (51)
Kunzea parvifolia	5	Warburton Rd (41)
Kunzea sp. C (aff. *capitata*)	5,7S	Near Pigeon Box (34)
Lasiopetalum parvifolium	3,7S*	Yowaka River (51)*, Bermagui
Laxmannia sessiliflora	5,7N*	Mt Nadgee (6), Saltwater Ck (7), near Sidlings Swamp (55)
Lepidium pseudotasmanicum	5	Kings Ridge Rd (8) 2km SW Pambula Beach (62)
Lepidosperma flexuosum	5	Lower Nadgee River (6)
Lepidosperma forsythii	5	Nadgee Lake (6), Sidlings Swamp (55), near Timbillica Stn (57)
Lepidosperma gladiatum	7N	Pambula [Jane Spiers Beach (6)]
Lepidosperma semiteres	7N	Saltwater Ck (7), Duck Hole Rd/Saltwater Ck Rd (7)
Leptorhynchos nitidulus	5,7S	Nahgi Rd (49), Eden
Leptospermum laevigatum	7LN	Green Cape (7)
Leptospermum myrsinoides	7N	Duck Hole Rd (7), Green Cape Rd (42)
Leptospermum polygalifolium	7S	Sheep Station Ck (31), Imlay Rd (57), Pericoe Rd (57)

APPENDIX (Cont'd.)

Species	Significance	Localities
Leptospermum scoparium	7N	Nethercote Falls (18)
Lepyrodia scariosa	5,7S*	Merrica River crossing (6), Nadgee Moor (6)*, Green Cape (7), Mt Nadgee (49)*
Leucopogon attenuatus	5,8	Nethercote Falls (18), White Rock Falls (37), Yowaka-Old Hut rhyolite outcrops (51), Mt Poole (57)
Leucopogon collinus	5,7LN*	Duck Hole Rd/Green Cape Rd (42)*, Yambulla catchments (57)
Leucopogon gelidus	5	Mt Imlay summit (9), Wog Wog Mtn (10), White Rock Mtn (10), near Mines Rd (49)
Leucopogon setiger	5,7S,8	Yowaka-Old Hut rhyolite outcrops (51)
Leucopogon suaveolens	5	Nalbaugh Plateau (10), Waratah gully (22), Cairnlea (37), Bull Mtn (44)
Lilaeopsis polyantha	5	Dragon Swamp (20), Sheep Station Ck (31), Tantawangalo Ck (44), Coolumbooka (60), Twofold Bay
Limonium australe	3	Wonboyn Lake (6), Wallagoot Lake (13), Bermagui River, Twofold Bay
Linum marginale	5	Nadgee (6), Yambulla catchments (57)
Liparis reflexa	7S	Murrah River tributary (61)
Livistona australis	5v	Grassy Hill (5), Bunga Head (8), Mumbulla Ck (46), Wapengo Ck (46), Tanja
Lobelia dentata	7S	Nadgee (6,49), Wangarabell Trail (57)
Logania pusilla	5v	Smiths Rd/Lizard Rd (46), Germans Ck (57)
Lomandra confertifolia ssp. *rubiginosa*	7S	Near Nadgee Moor (6)
Lomandra confertifolia ssp. *similis*	7S	Near Sandy Beach Ck (3)
Lotus australis	5	Tantawangalo (54), Nimmitabel (64), Bombala (64)
Luzula modesta	5	Eastern Bondi (37)
Luzula ovata	5	SW Nungatta Mtn (11), Dinner Ck (55)
Lycopodium varium	5v	Nalbaugh Plateau (10), Pheasants Peak (41)
Macrozamia communis	7S	Kianniny Bay (13)
Marsdenia suaveolens	7S	Waalimma Rd (57)
Mazus pumilio	5	Nadgee (6,49), Saltwater Ck (7), 'Nungatta'
Melaleuca hypericifolia	7S	Evans Hill (Tathra)
Mentha diemenica	5	Sheep Station Ck (31), Head of Reedy Ck (41), Brittens Trail (46), Candelo Ck (54)
Micromyrtus ciliata	5	Bemboka Walls (34)
Mimulus repens	5	Nadgee Lake (6), Wallagoot Lake (13), Bermagui, Twofold Bay
Mirbelia pungens	5	3.7km W Bemboka Peak (34), Yowaka-Old Hut rhyolite outcrops (51)
Mitrasacme serpyllifolia	3	Nunnock Swamp (20), Sheep Station Ck (31), Tantawangalo Mtn (54)
Monotoca elliptica	9	Mt Imlay summit (8)
Montia australasica	5	Bondi Gulf (25), Sheep Station Ck (31), Tantawangalo Ck (54)
Myoporum acuminatum	7S	Reedy Ck (41)
Myoporum bateae	3,7S*	Nelson Lagoon (8), Rocky Hall Trail (41), Mt Pericoe (28)*, 2km WNW Murrah River/Mumbulla Ck (61), near Wapengo Lagoon
Myosotis australis	5	Nadgee (6), Big Jack Mtn (41), Dragon Swamp Rd (54), head of Solomons Ck (54)
Notelaea longifolia	5,7S*	Bunga Head (8), Aragunnu Ck (8), Mt Pericoe (28)*, Eden
Notothixos subaureus	5v	Nadgee (6), Saltwater Ck (7), Bega area, 1 km S of Eden
Olax stricta	5v	Long Beach (7), Saltwater Ck (7), Green Cape (7)
Olearia alpicola	5	Waratah gully (22), S Rockton section (37), western Bondi in streamside reserve (37)
Olearia axillaris	5	Tura Beach (13), Bermagui area

APPENDIX (Cont'd.)

Species	Significance	Localities
Olearia glandulosa	5	Sheep Station Ck (31), S Rockton section (37), Compartment 1370 (40), Snob Ck (57)
Olearia rugosa	5,7N*	Nadgee Lake (6), Mt Imlay summit (9)*
Omalanthus populifolius	5,7S*	Bellbird Gully (1), Jane Spiers Beach (6), Head of Table Ck (6)*
Opercularia diphylla	5,7S	Twofold Bay (?7/42)
Oreomyrrhis ciliata	5	Dragon Swamp (20)
Oxylobium scandens	3,6,7S	3.2km NE Tanja (46)
Parietaria debilis	5	Mt Imlay summit (9), Stanton Rock (51)
Parsonsia straminea	5,7S*	Murrah River tributary (61), Wicks End catchment (44), Cebs catchment (44), Wilbob catchment (44)*
Pellaea falcata var. *nana*	5	Maxwells or Watergums Ck (?16/23), Lizard Rd (46), 3.5km NNW Sugarloaf (51)
Persicaria subsessilis	5	Nadgee (6), Palestine Ck (51), Nungatta
Persoonia brevifolia	2(2RCa),4,7N*	Mt Imlay summit (9), Wog Wog Mtn (10), Nalbaugh Plateau (10)*, Nungatta Mtn (11)
Persoonia juniperina	7N	Laings Rd (37)
Persoonia ('asperula' ms)	5v	Near Bega Swamp (59)
Phebalium carruthersii	2(3RC-),7S*	Mt Pericoe (28)*, 2km ESE Mumbulla Mtn (46), Lizard Rd (46), Dr George Mtn
Phebalium diosmeum	7S	Lower Table Ck (6), Top Moor (6)
Phebalium phylicifolium	5	Nunnock Swamp (20)
Phebalium ralstonii	1,2(2VCi)	Jingera Rock (4), Nethercote Falls (18), Yowaka-Old Hut rhyolite outcrops (15,51)
Phebalium rhytidophyllum	1,2(2VCit)	Nalbaugh Plateau (10)
Phebalium squamulosum ssp. *argenteum*	5v	Jane Spiers Beach (6), Michael Lagoon lookout -S of Bermagui
Phebalium squamulosum ssp. *squamulosum*	5	Head of Nadgee River (6), Maxwells Ck (16), Nahgi Rd (49)
Philotheca salsolifolia	5,7S*	Bemboka Walls (34)*, Desert Ck escarpment (34)
Pimelea curviflora ssp. *gracilis* var. *sericea*	5	Bemboka Walls (34), Bombala (64), Twofold Bay area
Plantago hispida	5	Mouth of Little Ck (6), Saltwater Ck (7), Tathra Beach, Twofold Bay
Platycerium bifurcatum	5,7S	Bunga Head (8)
Plectranthus graveolens	7S	2.5km S Burragate Pk (4), Reedy Ck (41)
Plinthanthesis paradoxa	5v	3km S Nadgee River (6), Impressa Moor (6), Duck Hole Rd (7)
Poa affinis	5,7S*	Mouth of Nadgee River (6)*, mouth of Little Ck (6), Nungatta (11)
Poa cheelii	5,7S*	Nethercote Falls (18)*, Yowaka-Old Hut rhyolite outcrops (51)*, Chalkhills Rd (58), Wapengo-Tanja, Cuttagee-Bunga
Poa costiniana	5	Dragon Swamp (20)
Poa helmsii	5	Imlay Rd (31), Packers Swamp Rd/Experimental catchment Rd (44)
Podocarpus spinulosus	5,7S*	The Pinnacles (7), Broadwater Rd (51)*
Pomaderris angustifolia	5	Nungatta (11), Genoa River (37)
Pomaderris betulina	5	Nadgee (6), Bunga trig (8), Wallagaraugh River/Imlay Ck (57), Yambulla catchments (57)
Pomaderris brogoensis	2(3RC-),4,7S*	Merrica River crossing (6)*, 6.7km E of Bemboka Peak (34), Brogo Pass (63), Twofold Bay
Pomaderris cinerea	7S	Mt Imlay (9)
Pomaderris costata	2(3VC-)	Jingera Rock (4), Mt Imlay (9), Neenah Ck (11), Pheasants Peak (41), eastern Coolangubra (41), Cebs catchment (44), Wicks End catchment (44), Mt Poole (57), Letts Mtn (57), upper Chalkhills Ck (58)
Pomaderris cotoneaster	2(3VC-)	Neenah Ck (11), Reedy Ck (41), Tantawangalo weir (54)

APPENDIX (Cont'd.)

Species	Significance	Localities
Pomaderris discolor	5v	Wallagaraugh River (57), 1 km S Pambula (62), Wog Wog Stn
Pomaderris elachophylla	5,7N*	Nalbaugh Plateau (10), Myanba Ck (41), near Tantawangalo Mtn (54)*
Pomaderris eriocephala	5	Genoa River (11,37), upstream of White Rock Falls (37), Tantawangalo Ck/Postmans Trail (46), Tantawangalo Weir (54)
Pomaderris ledifolia	5v	Yowaka-Old Hut rhyolite outcrops (51), Mt Poole (57), 4.8km W Mt Poole (57)
Pomaderris parrisiae	2(2VC-),4,7S*	Jingera Rock (4)*, Green Cape Rd (?7/42), Pipers Lookout (14), Big Jack Mtn (41), Wilbob Ck track (46)
Pomaderris pauciflora	2(3RC-)	Genoa River (11), White Rock River (37)
Pomaderris virgata	2(2RC-),4,7S*	Jingera Rock (4), 1.6km SW Burragate Peak (4), Wog Wog Mtn (10), Jingera (15), Mumbulla (46), 2.5km NE Mt Poole (57)*, Wolumla Peak (58), Dr George Mtn (53)
Pomaderris sp. aff. *andromedifolia*	3,7S*	Merrica River crossing (6)*, Wallagaraugh River/Imlay Ck (57)
Pomaderris sp. aff. *cinerea*	3,4,7S*	Bemboka (34), Reedy Ck (41)*, Tantawangalo Ck (46)
Prasophyllum sp. aff. *morrisii*	1,2(2E)	Old Hut Ck rhyolite outcrop (51)
Pratia pedunculata	5	Waratah Ck (22), Head of Chalkhills Ck (58)
Prostanthera decussata	5v	Nadgee (6), eastern Coolangubra (41), Yambulla catchments (57)
Prostanthera nivea	5	Yowaka-Old Hut rhyolite outcrops (15), Nethercote Falls (18), Lochiel
Prostanthera ovalifolia	5,7S*	Harrys Hut (6), Bemboka Walls (34), Desert Ck escarpment (34), 4km NE Mt Nahgi (49)*
Prostanthera phylicifolia	5	Jingera Rock (4), Yowaka-Old Hut rhyolite outcrops (51), Mt Poole (57)
Prostanthera rotundifolia	5	Nadgee (6), upstream of White Rock Falls (37), Genoa River (37), Yowaka-Old Hut rhyolite outcrops (51)
Prostanthera sieberi	5,7S	3km E Bega-Bermagui Rd (?8/46/48), Dr George Mtn
Prostanthera walteri	2(3RCa),7N	Mt Imlay (9), Nalbaugh Plateau (10)
Pseudanthus divaricatissimus	2(3RCa)	Merrica River crossing (6), Newtons Crossing (6), 2 km ESE Narrabarba (17), Nethercote Falls (18), Yowaka-Old Hut rhyolite outcrops (51), Mt Poole (57)
Pseuderanthemum variabile	7S	Nelson Ck (8), Mumbulla Ck Rd (46)
Psoralea adscendens	5	Cairnlea (37), W of Big Jack Mtn (41), Packers Swamp Rd (46), Cathcart
Psychotria loniceroides	7S	Wapengo Ck (46)
Pterostylis plumosa	5,9	Green Cape (7) — coastal occurrence
Pultenaea altissima	5v,9*	Nungatta Ck-Genoa River (11) — low altitude locality*, Nunnock Swamp (20)
Pultenaea benthamii	7N	Bemboka River headwaters (44)
Pultenaea blakelyi	5,7S	S end Black Range (3), N of Milligandi Rd (52)
Pultenaea capitellata	5v	Nunnock Swamp (20), Tantawangalo Mtn (54)
Pultenaea dentata	5	Impressa Moor (6), Nadgee Lake (6), Cape Howe (6), Sheep Station Ck (31)
Pultenaea elliptica	5,7S	Nutleys Ck (48)
Pultenaea hispidula	5	Tura Beach Rd (13), Watergums Ck (49), 1.5 km N Merimbula
Pultenaea paleacea var. *sericea*	5	Endeavour Moor (6), Sheep Station Ck (31), upper Genoa River (?37)
Pultenaea paludosa	5v	Nadgee (6), Duck Hole Rd (7), near Mt Imlay (?42/55), Compartment 425 (57)
Pultenaea subspicata	5v	Mt Darragh (?40/54)
Pultenaea subumbellata	5	Nalbaugh Swamp (10), Sheep Station Ck (31), Brown Mtn area (44)
Pultenaea villifera	2(3RC-),7S,8	Yowaka-Old Hut rhyolite outcrops (15,51)
Ranunculus inundatus	5	Nungatta Ck (11), Walla Walla Trail (57)
Ranunculus pimpinellifolius	5	Dragon Swamp (20), Sheep Station Ck (31)

APPENDIX (Cont'd.)

Species	Significance	Localities
Ranunculus rivularis	5	Sheep Station Ck (31), Wog Wog trail (41), Tantawangalo Ck (44), swamps near Brown Mtn (44), Coolumbooka (60)
Restio tetraphyllus ssp. *tetraphyllus*	5,7N*	Merrica River (6), Green Cape Rd (7/36)*, Nadgee (49)
Rhagodia candolleana	9	Reedy Ck (41), Willeroo (65) — non-coastal localities
Rorippa dictyosperma	5	Brown Mtn (?14/44)
Rulingia hermanniifolia	2(3RCa),7S,8	Yowaka-Old Hut rhyolite outcrops (15), Nethercote Falls (18)
Santalum obtusifolium	5	S end Black Range (3), 1.2km S Grassy Hill (5), Nadgee (6), Mumbulla Ck/Murrah River (46), Wolumla Pk Rd/Pambula River (58), Rocky Hall trail
Sarcochilus australis	5,6	Lower Nadgee River (6), Stanton Rock (51), Letts Mtn (57), Bega area
Sarcochilus hillii	6	Murrah River tributary (61), Tathra
Sarcochilus olivaceus	5,6,7S*	Nadgee River (6)*, Bunga Head (8), heads of Maxwells & Royds Cks (16)* Mumbulla (46), Murrah River tributary (61)
Sarcomelicope simplicifolia	5,7S	Murrah River tributary (61)
Scaevola albida	5	Swamp in Nadgee (6), Yambulla catchments (57)
Scaevola calendulacea	5,7S	Newtons Beach (6), Bermagui
Schizomeria ovata	5,7S	2km WSW Horses Head Rd/Murrah River Rd (48)
Schoenoplectus validus	5	Swamp in Nadgee (6), Bega River (63), 10km NW Towamba (65)
Schoenus moorei	5,7S*	Near Wonboyn (6), Impressa Moor (6)*, Saltwater Ck (7)
Schoenus nitens	5	Merrica River crossing (6), near Newtons Beach (6), Cape Howe (6), Nelson Lagoon (8)
Schoenus pachylepis	7S	Impressa Moor (6)
Schoenus turbinatus	5v	Mt Victoria trig (6), Edrom Rd (42), Mt Naghi (49), Yambulla catchments (57)
Schoenus villosus	5,7S	Top Moor (6)
Scleranthus biflorus	5	Sheep Station Ck (31), Dragon Swamp (20), Bull Mtn (46), Coolumbooka (60)
Sclerostegia arbuscula	5	Nelson Lagoon (8), Wapengo Lagoon, Merimbula
Scutellaria humilis	5	Stanton Rock (51), Two Bridges Ck (54)
Senecio glomeratus	5	Cape Howe (6), Nunnock Swamp (20), Sheep Station Ck (31)
Senecio spathulatus	5,7N	Cape Howe (6)
Senecio squarrosus	5	Cape Howe (6)
Sicyos australis	5v	Narira Ck (12), Rocky Hall Trail (41), Kiah (65), Bega area (?63)
Solanum stelligerum	5,7S*	Mouth of Narira Ck (12), Short Point Beach (Merimbula)*
Solenogyne gunnii	5	Sth Ben Boyd (7), Big Jack Mtn (41), Coolumbooka (60)
Sparganium subglobosum	3	Sheep Station Creek (31), Brockelos Ck (48)
Spyridium cinereum	2(3RCa)	Newtons Beach-Little Ck (6), 1.5km N Nadgee River (6), Endeavour Moor (6)
Stellaria angustifolia	5	Nungatta (11), Sheep Station Ck (31), Reef Ck (37), western Bondi in streamside reserve (37), Imlay Ck (57)
Stellaria multiflora	3	Stanton Rock (51)
Stephania japonica var. *discolor*	7S	2.5km N of Haycock Hill (7), Nungatta (11)
Sticherus flabellatus	5v	Bellbird Ck (1), Merrica River (6), Sth Ben Boyd (7), Yowaka-Old Hut rhyolite outcrops (51)
Sticherus tener	5	Nadgee (6), Nungatta (11), Watergums Ck (23)
Stipa semibarbata	5	Nadgee (6), E of Nunnock Swamp (20)
Styphelia adscendens	5	Imlay Rd (37), near Wallagaraugh River (57)
Styphelia sp. 1	2(3RC-),7S,8	Nalbaugh Plateau (10)
Symphionema paludosum	5,7S*,8	Nadgee River (6)*, Table Mtn (6), Mt Nadgee (6,49)*, Duck Hole Rd (7)
Symplocos thwaitesii	5v	Wapengo Ck (46)

APPENDIX (Cont'd.)

Species	Significance	Localities
Synoum glandulosum	7S	1.5km W Tathra Rd/Neilsen Rd (8), 4km W Dr George Mtn (63)
Tetrarrhena acuminata	3,7N*	Head of Merrica River (6), Nalbaugh Swamp (10)*, near Bondi Gulf (37)
Tetrarrhena turfosa	5	Nalbaugh Swamp (10), Sidlings Swamp (55)
Tetratheca labillardierei	5	SW spur Nungatta Mtn (11)
Tetratheca subaphylla	3	Mt Imlay summit (9), Nalbaugh Plateau (10), Big Jack Mtn (41), Goanna Rd (42), Yowaka-Old Hut rhyolite outcrops (51)
Tetratheca thymifolia	7Sv	Stringy Rd/Maxwells Rd (49)
Thelionema umbellata	5v	Nadgee (6,49), Nunnock Swamp (20), Warburton Rd (41)
Thysanotus juncifolius	5	Top Moor (6), 8km N Eden (?7/51)
Tmesipteris ovata	5v	8km E Timbillica (16), Nadgee (49)
Tmesipteris truncata	3,7S	SE of Burragate Peak (4)
Trachymene humilis	5	Cairnlea (37), MacLaughlin River (64)
Tricostularia pauciflora	5	Newtons Beach-Little Ck (6), Yambulla catchments (57), Wallagaraugh River/Princes Hwy
Trisetum spicatum	5	Dragon Swamp (20)
Tristaniopsis collina	5,7S	Murrah River Rd (48)
Trochocarpa laurina	5,7S	Murrah (48)
Typha domingensis	5	Pipeclay Ck -S of Pambula (63)
Utricularia lateriflora	5	Nadgee (6), White Rock River (37), Bens Ck (55), Indigo Ck crossing (57)
Velleia montana	5	Nunnock Swamp (20)
Vernonia cinerea	7S	Saltwater Ck (7), Sheep Station Ck (31)
Villarsia exaltata	5	Nadgee Lake (6), Cape Howe (6), Sth Ben Boyd (7)
Villarsia reniformis	5	Nunnock Swamp (20), Snob Ck (31), Timbillica (55), northern Yambulla (57)
Viola caleyana	5v	Nunnock Swamp (20), Sheep Station Ck (31)
Viola cleistogamoides	5,7N	Wonboyn (?6/49)
Vittadinia cuneata var. *cuneata*	5	Goats Knob Rd/Neilsen Rd (8), Nelson Lagoon (8), Pambula River (62), Eden area
Wahlenbergia gloriosa	5	Bega Swamp (59), 9km E Cathcart (64)
Wahlenbergia luteola	5	Mt Imlay (9)
Wahlenbergia multicaulis	5	Nimmitabel-Brown Mtn (?46/64)
Westringia davidii	1,2(2V)	Yowaka-Old Hut rhyolite outcrops (15,47,51)
Westringia fruticosa	7S	Nadgee Lake (6)
Wilsonia backhousei	3,8	Bermagui, Twofold Bay
Xanthorrhoea concava	7S	Wangarabell Rd (57), Yambulla catchments (57)
Xanthosia atkinsoniana	5,7S	Bermagui (2), 1 km SE Boundary Bridge (5), Dignams Ck-Wallaga Lake (12), Murrah (48)*
Xanthosia pusilla	5,7N*	Impressa Moor (6), Bay Cliff (6), Green Cape (7)*
Zieria arborescens	5	Wog Wog Mtn (10), Nethercote Falls (18), Wandella Ck (27), Big Jack Mtn (41), Rocky Hall (?41/65)
Zieria cytisoides ssp. *cytisoides*	5,7S*	Bemboka Walls (34), Big Jack Mtn (46)*, Mumbulla Mtn (46)
Zieria cytisoides ssp. *littoralis*	4v,7N*,9**	Disaster Bay (6), Jane Spiers Beach (6), Green Cape (7), Saltwater Ck (7), Bengunnu Pt (8) Bunga Head (8)*, Bournda (13), Narrabarba Hill -non littoral locality (17)**, Jews Head (S of Eden), Tathra
Zieria fraseri ssp. *compacta*	5,7S*,8	Nethercote Falls (18)*, Bemboka Walls (34)
Zieria pilosa	5,7S	3km W Saltwater Ck (7)
Zieria sp. 7	1,2(2E)	Lochiel
Zieria sp. 14	1,2(2E)	Box Range, north (W of Pambula)
Zieria sp. 15	1,2(2E)	Box Range, south (W of Pambula)

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Haemoglobin in Plants: Evolution really is Conservative

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(Delivered by J. PEACOCK 11 October 1989)

It is a pleasure for me to be giving the Linnean MacLeay Lecture, particularly because I was a Linnean MacLeay Fellow during my PhD program in this University. At that time my research concerned the evolution of the Australian flora. I was concentrating on one family, the *Goodeniaceae*, under the guidance of Professor Spinney Smith-White whom I am sorry is not able to be here tonight.

One of the critical tools we used in making deductions about relationships between species and genera within the plant family was the number of chromosomes in the genome. I can remember looking at countless chromosome spreads and wishing that I could be down inside the nucleus looking at gene activity, thinking that if I could really look at genes I'd be able to say much more about the relationships of species and how evolution really worked.

That may have been a naive dream at the time but what I'd like to discuss this evening is the achievement of that dream. These days we are able to look at genes; not only at their genetic structure and the map of their genetic code but also we are having some considerable success in understanding how their activity is controlled.

Controlled patterns of gene activity are really the major determinants of development.

I am privileged to work with some wonderful colleagues in CSIRO, and we and many other laboratories working in this gene engineering field have been struck by the power of selection and the conservation of successful molecular strategies over huge distances within the evolutionary fabric.

The examples I am about to give you on gene sequence and structure and of the systems which control gene activity are comparable to the morphological and physiological characters that have taught us so much about evolution in the past. But to me the new observations are more emphatic because we are looking at properties of the prime genetic material. My examples are from our own laboratory but I want to emphasise that much of what I have to say is paralleled and often depends upon work in many other laboratories around the world.

One example I think you will find interesting concerns the molecule which gives our blood its characteristic red colour, haemoglobin. Haemoglobin is important in many animals for oxygen transport and it is also found in plants. Until fairly recently it was known only in nodules on the roots of legumes. These are structures that are formed in a symbiotic relationship between the bacterium *Rhizobium* and the host plant root tissue. They are important for the fixation of atmospheric nitrogen for the plant. I hasten to add, because this is a Sydney audience, that the plant that you know in our own flora, *Hemadorum*, with its brilliant red tissue, is not a plant with a lot of haemoglobin; the orange red colour is another pigment molecule.

The haemoglobin in nodules, where does it come from? It is produced by the plant tissue. Initially, when the amino acid sequence was determined, it appeared that

there were striking similarities between the legume haemoglobin molecule and the haemoglobin in animals. In particular, critical amino acids involved in folding of the molecule, in forming bonds with the haem moiety, and in forming the O_2 pocket, were identical in the plant and animal molecules. But it was when the plant haemoglobin gene was analysed that really striking identity emerged.

As you may know, genes in plants and animals often have an interrupted genetic code structure, with alternating exons and introns. There are three introns in the leghaemoglobin gene. The first and third introns are in precisely the same positions as the two introns in animal haemoglobins. The central intron is at the spot where protein chemists had predicted from the domain structure of the animal haemoglobin that another intron could have been expected. This was on the basis of the supposition that introns are involved with the construction of genes from component sequences. This lego theory of gene construction has considerable support.

It was realised that this identity was not likely to have been by chance. There were basically two explanations. Both assume that the genes were related by evolutionary descent. In one case we can assume a linear descent from a progenitor of plants and animals. On the other hand we can propose transfer of the gene from the animal kingdom into the legumes during the evolution of the symbiotic relation between the bacteria and the legume plant. Insects were considered to be a possible donor.

The plot thickened when the haemoglobin molecule was found in other plants, plants which have nodules that fix nitrogen — *Casuarina* is a good example, and another one is *Parasponia* which is a member of the elm family. There are many other examples known, scattered throughout the dicotyledons. Initially haemoglobin was not detected, but subsequently with better biochemistry, it has been shown that haemoglobin is present in the molecules in each species.

A couple of years ago we isolated the haemoglobin genes, initially from *Parasponia* and then later from *Casuarina*. Their sequence and intron positions left little doubt that all plant haemoglobin genes are closely related. This obviously placed some strain on the horizontal evolution hypothesis of haemoglobins into plants and strongly favoured the linear descent concept. In thinking about this we wondered whether this meant, since the phylogenetic distribution of nodulated plants is so scattered, that previously all plants were nitrogen-fixing and were nodulated, with only a few species in several families being the relics of this condition. Or could it mean that in fact all plants have a haemoglobin gene, presumably with a function or functions in a normal plant. Particular plants would have evolved a symbiotic relation with *Rhizobium* or with *Franckia* or some other bacteria independently in different families or groups of families. This latter alternative is much more attractive in an evolutionary sense and on a lot of morphological grounds too with respect to the structure of nodules and the biology of the symbiotic relationships.

We then looked at some plants that were known not to nodulate and asked whether they have a haemoglobin gene present and in a functioning form. It is difficult to look for the molecule if it is in very low amounts. The isolation of haemoglobin is no simple task from plant tissue. There are antibodies for haemoglobin but the trouble is that haemoglobin, although having certain key regions highly conserved, is a protein which permits a substantial amount of amino acid substitution, presumably without disrupting functional aspects of the molecule. The antibody is likely then to have limited phylogenetic reach. The antibody will only react where proteins are fairly closely related and have the same epitopes.

Similarly, we would expect that nucleic acid probes would have a limited taxonomic reach too. The amino acid substitution variation means that we can expect a lot of mutation substitution in the DNA sequences, and this is the case. Initially we started

with a particular family. We chose the elm family where both nodulated and non-nodulated species and genera were known. We found that *Trema*, a genus closely related to *Parasponia* but which does not nodulate, does have a haemoglobin gene and it is a functioning gene. So too does another genus, *Celtis*, and we think that *Ulmus* itself also has the gene. On this basis we feel it is likely that all plants have a haemoglobin gene.

We asked first in *Trema* where the gene did function in the plant. Initially we checked stem, root and leaves and found expression, detecting both messenger RNA and protein, only in the roots. The fact that there was tissue-specific expression suggested that this haemoglobin must have a particular function or functions, hitherto unsuspected in plants. We have not looked extensively in other tissues but there has been a report of haemoglobin in the seed of the winged bean. In *Parasponia*, the single haemoglobin gene is expressed in large amount in the nodules and to a much lower level in the roots. There must be two different controls operating.

We took our analysis a little further by making transgenic plants, introducing the *Trema* and the *Parasponia* genes into tobacco. We found that the gene was expressed in the roots of the transgenic tobacco plant. The genes, when introduced into *Lotus*, a legume, were expressed in both the nodule and in the root.

At this stage I need to say a little bit more about the structure of a gene. As well as the coding region which determines the gene product, another important property that has become clear in recent years is that there is an upstream region in the DNA molecule, immediately adjacent to the coding region, which contains most of the signals important in determining the time, place and amount of gene expression.

When we placed the *Parasponia* and *Trema* genes into tobacco, or even just their control regions hooked to a reporter gene, which enabled us to determine easily where the gene was working, the results indicated that the gene controls, which evolved in the elm family of plants, were working perfectly well in the transgenic legume and in transgenic tobacco.

There are two components in an effective gene control element; the DNA target sequence and a binding protein. Our results implied that the tobacco plant has the machinery to correctly control the expression of the *Ulmaceae* haemoglobin gene; presumably it has its own haemoglobin gene, highly homologous to those we inserted by genetic engineering. Our conclusion is that almost certainly the primitive condition in plants is that there is a haemoglobin gene in the genome and that the gene product has one or more functions in certain plant tissues. We suspect that this is probably the case in all plants.

What could that function be? Initially, we judged by the very small amount of haemoglobin present in roots, that unless there was localization to particular cells there was not enough haemoglobin present for it to act as an oxygen carrier, the same way it does in nodules. We wondered whether it might be an oxygen sensor molecule. Using the reporter genes that I talked about before we found that expression is localized to particular cells in the root, so the possibility that it acts as an oxygen carrier is still a viable alternative. The take-home message is that the conservatism of evolution is beautifully shown by the haemoglobin genes; it is highly probable that both the animal and plant kingdom variants have evolved from a common ancestor organism which preceded the separate evolutionary paths of the animal and plant kingdoms. Recent data suggest that the gene may extend back to proto-organisms occurring some 3-5 billion years ago.

I want to push these molecular examples a little further now by giving you another story from our lab, concerning gene controls. I think the conservatism of controls of gene action provides perhaps the most striking evidence of the powers of selection and the opportunism of evolution that I have seen in molecular analyses of the genome. We

have been studying an important biochemical response in plants. When roots are flooded, oxygen is excluded from the cell environment and plants switch their metabolism from an oxidative breakdown of carbohydrate to a fermentative pathway; there is a remarkable cessation of protein synthesis followed by a selective synthesis of anaerobic proteins, which have been identified as the enzymes of the fermentation pathway. One of the critical enzymes is alcohol dehydrogenase (Adh), now probably the best known gene system in plants. We chose originally to study it, not only because of its presence in this particular facet of plant biochemistry, but because there were some strong genetic tools available to us. The alcohol dehydrogenase gene structure, quite a complex one with nine introns, is conserved through the plant kingdom.

With regard to the control of this enzyme, what we did was to do some genetic surgery in the upstream region, making deletions, and then putting the deleted gene back into plant cells and asking whether it could still work in the right way. We were able to define a small, critical region that donated the property of anaerobic response in the transcription of this particular gene. If we took that small region, the anaerobic response element — the ARE — and put it in front of another gene then the target gene came under anaerobic induction control. The ARE has a highly conserved core hexamer, TGGT T T, and we found this present in the critical ARE regions of every other alcohol dehydrogenase gene we have looked at in both monocot and dicot species. Interestingly it is also present in the control regions of the other genes that are under anaerobic control, for example in the aldolase and sucrose synthase genes. This is an example of where a particular control region has been used to bring about coordinate expression of genes in order to achieve a complex biochemical response.

The aldolase gene also demonstrates a point I mentioned earlier, that genes have been put together in the way that a child builds a lego construction. We suspect that maize aldolase provides us with an example of an upstream control region being hooked to an existing aldolase sequence in order to give it an anaerobic induction property.

This same anaerobic control we characterized in plants is now being found in anaerobically controlled genes in fungi and even in bacteria. A wonderful example of the way in which selection has maintained something that has the right properties. The striking thing to me is that selection can be so tight that it preserves a sequence of just six nucleotides.

But, I want to stress that the conservatism isn't just in DNA sequences. Remember I mentioned before that the control sequence that we are looking at is a target sequence. DNA binding proteins recognize particular target sequences and it is the combination of the bound protein and the DNA sequence that provides the control switch. In fact there are usually a number of control components which interact to give an effective transcription unit to provide the signal for the RNA polymerase molecule to proceed down the DNA double helix transcribing a messenger RNA. In probing the anaerobic induction control of Adh, we asked whether the maize control would work in transgenic tobacco. We were initially disappointed to find that it hardly worked at all. But when we added an enhancer sequence, a sequence which increased the amplitude of gene response, we found the maize ARE worked fine in tobacco. In this case the combination of the enhancer sequence and the ARE were necessary to give a high intensity and well controlled response.

I have mentioned this because we have recently put a lot of effort into examining the protein that binds to the enhancer sequence. Of course this DNA binding protein is itself encoded by a gene. Our surprise was that when we isolated and sequenced the gene, we found, in the deduced protein sequence, extreme similarity to the amino acid sequences of binding proteins known in animals and in yeast. There is a particular class of DNA binding protein called a leucine zipper. The name comes from a regular spacing

of leucine residues in part of the protein molecule concerned with dimerization — two polypeptides associate together to form a dimer which is the functional protein. It is thought that the leucines interact in much the same way as two sides of a zipper. Adjacent to the leucine zipper region in the protein is a region of basic residues which is the region that recognizes and binds to the target DNA sequence. Elsewhere in the protein, in some proteins towards the N terminus and in others towards the carboxy terminus, there is a region, the activating region, involved in the interactions to make the effective transcription unit.

The remarkable thing is that many genes in the animal, plant and fungal kingdoms have used and maintained, with an extraordinarily high degree of conservation, this control system. It is a beautiful example of co-evolution, with conservation of both the DNA target sequence and the sequence of amino acids in the protein, important in bringing about the DNA-protein interaction. The system has been used in the different organisms to control different classes of genes. The GCN4 case in yeast is common to many genes involved in amino acid biosynthesis pathways; c-JUN and other related proteins in animals are concerned with control of a number of basic cellular processes. In fact c-JUN is an oncogene — when it is under imperfect control itself it can lead to induction of cancers.

We as yet don't know how this particular enhancer sequence is used in plant metabolism. One thing we do know is that pathogens of plants, including both *Agrobacterium* and certain plant viruses, have trapped this highly efficient transcription control to use for their own purposes.

I have tried to give you a present-day look at one property of life. Even at the finest levels of examination of the primary genetic material, and of the control functions for that primary code, evolution has been innovative but conservative. These striking cases of evolutionary conservatism in gene coding sequences, control target sequences and control binding protein gene sequences are all compatible with a single origin of life forms. The story which is unfolding in an exciting and rapid way, is that fundamental controls of gene action underlie the intricate patterns of development in plants, animals and micro-organisms. Differential cell futures depend on differential control of transcriptional activity of genes. This is not the only mechanism involved in the control of development but it is one of the major ones. For further background on the topics discussed above I would refer you to Appleby *et al.* (1988a,b, 1989), Landsmann *et al.* (1988) and Peacock (1989).

The work plan of evolution is like the Button plan for Australia's car industry. Different lifeforms use and rely upon the same basic components!

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Raised Marine Terrace on North-west Coast of Macquarie Island

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SELKIRK, P. M., ADAMSON, D. A., & WILSON, M. E. Raised marine terrace on north-west coast of Macquarie Island. *Proc. Linn. Soc. N.S.W.* 112 (3), 1990: 141-152.

Bathymetric data off the north-west coast of Macquarie Island shows a wide, gently sloping marine terrace extending offshore for up to 4600m. The submerged terrace is an extension, without change of average slope, of the onshore terrace. We consider that the whole terrace was formed during the period of rapid rise in sea-level following the last world-wide glacial maximum of the terminal Pleistocene. During the period from about 16 000 to 8000 years ago the combination of vigorous erosive action by the Southern Ocean, the fractured bedrock and the rise in sea-level accounts for retreat of the cliffs bounding the western edge of the island's plateau at an average of c.0.5m per year. Since world-wide sea level stabilized, continuing tectonic uplift at approximately 3mm per year has lifted the landward third of the terrace above sea-level.

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INTRODUCTION

Subantarctic Macquarie Island, 54°S 159°E, is an above-sea portion of the tectonically active Macquarie Ridge. Macquarie Island is uplifted oceanic crust from the eastern margin of the Australian plate (Williamson, 1988). Differential movement between the Australian and the Pacific plate is the source of the moderately high seismic activity along the Ridge (Jones and McCue, 1988).

Recognition of cobble and pebble beaches of marine origin, now raised significantly above sea-level (Varne, Gee and Quilty, 1969; Ledingham and Peterson, 1984) indicate that uplift of the island's surface above sea-level is relatively recent. Evidence from a variety of sources has allowed calculation of uplift rates for various parts of the island.

Studies of peat and penguin bones (McEvey and Vestjens, 1973) allowed Colhoun and Goede (1973) to calculate a maximum rate of 4.5mm per year and a minimum rate of 1.5mm per year, for beach terrace uplift at Bauer Bay and Green Gorge. Bergstrom's (1985) studies of peats in the Green Gorge basin allowed calculation (Selkirk, Seppelt and Selkirk, 1990) of uplift rates of 2mm and 5mm per year. From the height of the landward edge of the rock-cut marine terrace north of Bauer Bay, and assuming approximate stability of sea-level for the last c.6000 years, Adamson, Selkirk and Colhoun (1988) calculated uplift rates between 1.7 and 3.3 m per year.

The island is composed of a number of blocks likely to have moved vertically, or to have tilted, at different rates and to different extents relative to each other during the overall uplift process. A north-west-trending fault crosses the isthmus — separating Wireless Hill from the rest of the island. From studies of a peat deposit overlying a raised beach, Selkirk, Selkirk and Griffin (1983) calculated an uplift rate of 14.5mm per year for a Wireless Hill site. Bye (1988), using data from tide gauge measurements in Buckles Bay, calculated an apparent rate of uplift of the tidal datum of between 6 and 13mm per year, commenting that this is of the same order of magnitude as the uplift rate calculated for nearby Wireless Hill.

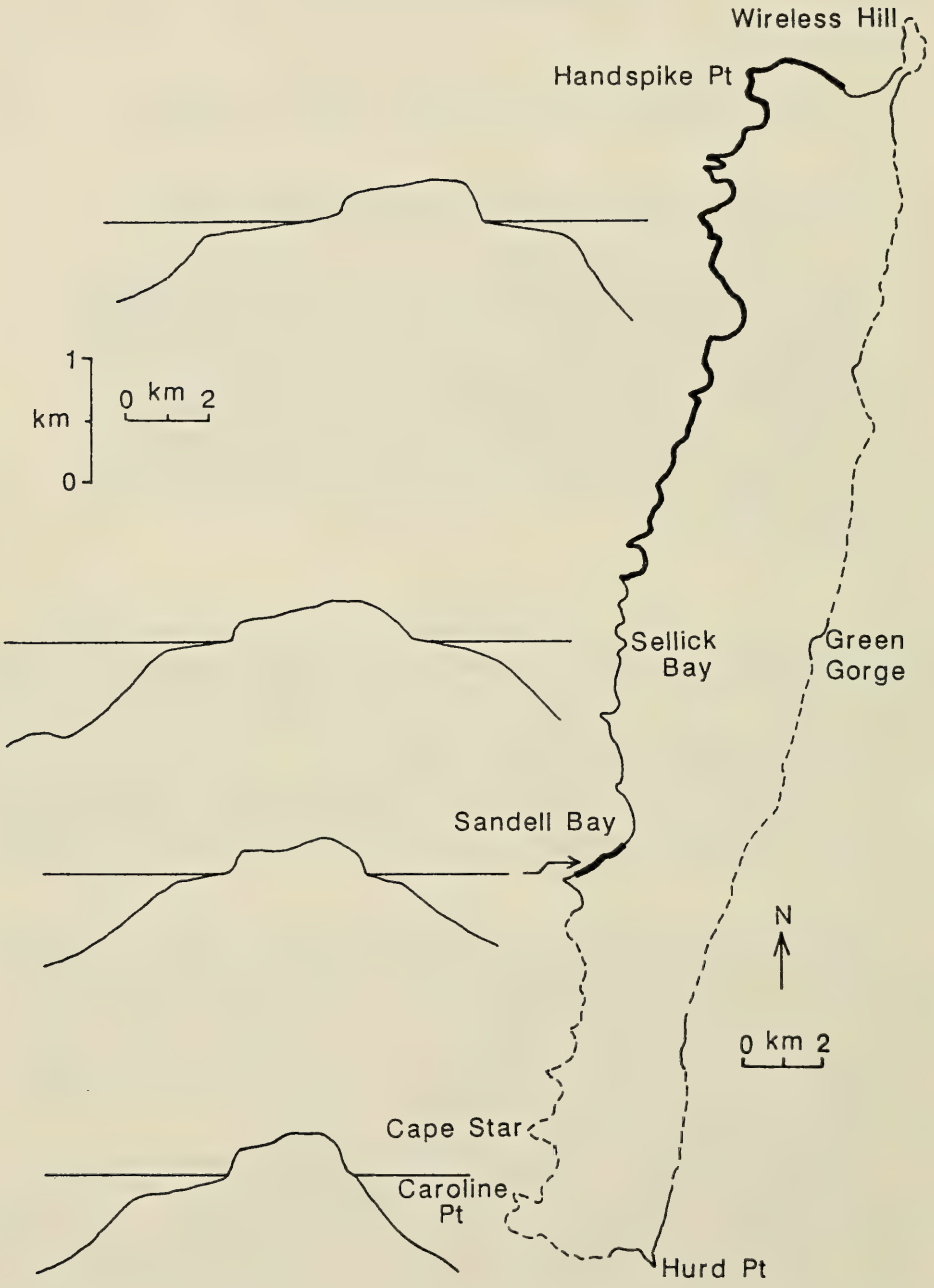

Fig. 1. (**a**) The coastline of Macquarie Island divided into three categories: wide marine terrace (thick line), medium width marine terrace (thin line), narrow or no marine terrace (dashed line). Terrace width is variable from bays to headlands, and although precise values for the width categories are difficult to allocate, in general a wide terrace would be several hundreds of metres and a narrow terrace would be less than 50 m in width. (**b**) Four east-west sections of the island and adjacent ocean floor.

Wide Marine Terrace

At the north-west corner of the island, and extending along the northern half of the west coast, a wide, gently sloping terrace extends from the shoreline to about 15 to 20m a.s.l., terminating at the base of the cliffs which bound the plateau (Fig. 1). Here the terrace is several hundred metres wide (Fig. 2, 3, Table 1). Other parts of the coast are bounded by a narrower terrace of similar form (Fig. 1, 4) or by cliffs which plunge directly into the ocean (Fig. 1, 5).

Fig. 2. Wide marine terrace at Half Moon Bay, photographed from plateau above Handspike Corner, looking southwards to Elizabeth and Mary Point, Eagle Point, Unity Point and Langdon Point. Plateau on left is approx. 200m a.s.l.

Fig. 3. Bauer Bay, photographed from plateau edge, retains sand carried from the plateau by Bauer Creek (bottom right of photograph). Washed rock surface of the wide marine terrace between Bauer Bay and Douglas Point (top right of photograph) is partly mantled by mire vegetation and ponds. Rock stacks rise above the average slope of the terrace).

Adamson, Selkirk and Colhoun (1988) described the nature of the surface of the terrace near Bauer Bay. They proposed that the terrace had been cut during a period of severe marine erosion of coastal cliffs between c.16 000 and c.8000 BP when world-wide sea-level was rising faster than uplift of the island. During the period of substantially stable sea-levels since c.6000 BP the terrace has progressively emerged from the sea as uplift of the island has continued. From their hypothesis for the terrace's formation, Adamson, Selkirk and Colhoun (1988) presented a model which predicted that the terrace extends undersea offshore to a total width of 1000 to 3000m, with the seaward edge of the terrace now 70 to 100m below present sea-level. This paper presents evidence from offshore to test these predictions.

Nearshore Bathymetry

Published bathymetric data for the area adjacent to the island are few (British Admiralty Chart No. 1022; Mawson, 1943). From these it seems that the seafloor slopes away from the island more steeply to the east than to the west, but nearshore configuration of the sea floor immediately to the west of the island was not known. Profiles across the Macquarie Ridge (Mawson, 1943) showing a shelf gently sloping for approximately 6km to the west of the island before a change to a steeper slope are, in the western portion, conjectural. 'Soundings off the west coast, except at the north end, are not sufficiently numerous to obtain a clear picture of the bottom contour adjacent to the Island. The soundings taken on that side of the Island do, however, demonstrate that . . . shallow water extends over a wide area' (Mawson, 1943).

Table 1

Measured and calculated parameters for 5 traverses across submerged marine terrace, north-west coast of Macquarie Island. Traverse locations shown on Fig. 6, profiles in Fig. 7

Traverse no.	Bearing (°)	Offshore width (m)	Depth of offshore edge (m)	Underwater slope	Onshore width (m)	Total width (m)
1	270	2100	70	1.9	600	2800
2	281	1400	90	3.7	500	1900
3	295	2500	100	2.3	1100	3600
4	305	4000	100	1.4	700	4700
5	339	4600	90	1.1	900	5500

From these 5 traverses, average offshore width = 2920m, average depth of offshore edge = 90 m, average underwater slope = 2.1°, average total width = 3700m.

Bathymetric data available to December 1970 were compiled by the Antarctic Mapping Branch, Division of National Mapping into a manuscript map. Additional bathymetric data for the vicinity of Macquarie Island, including to within 1.5km of its north-west coast, became available as a result of a Bathymetric Survey Program from MV 'Cape Pillar' in January 1982 (Manuscript Bathymetric Map, Division of National Mapping, 1982). Profiles across the island and the nearshore seafloor (Fig. 1) and a bathymetric map for the surrounds of the northern third of the island have been constructed from these sources (Fig. 6).

Testing the Terrace Formation Model

In order to test the predictions of Adamson, Selkirk and Colhoun's (1988) model, depth to the seafloor was determined along five traverses between Handspike Corner

Fig. 4. Medium width marine terrace at Hurd Point, looking east and showing uniform gentle seaward slope and emergent rock stacks.

Fig. 5. Coast at Cape Star with no terrace but rock stacks emerging from the ocean. Looking northwards from above Caroline Cove hut.

and Bauer Bay (Fig. 6) and across the course of MV 'Cape Pillar'. Depth soundings were taken from an amphibious vehicle (LARC) whose positions were plotted from compass sightings by three observers, one each at Handspike Point, Langdon Point and Mawson Point. Radio contact was maintained between LARCs and observers. The courses

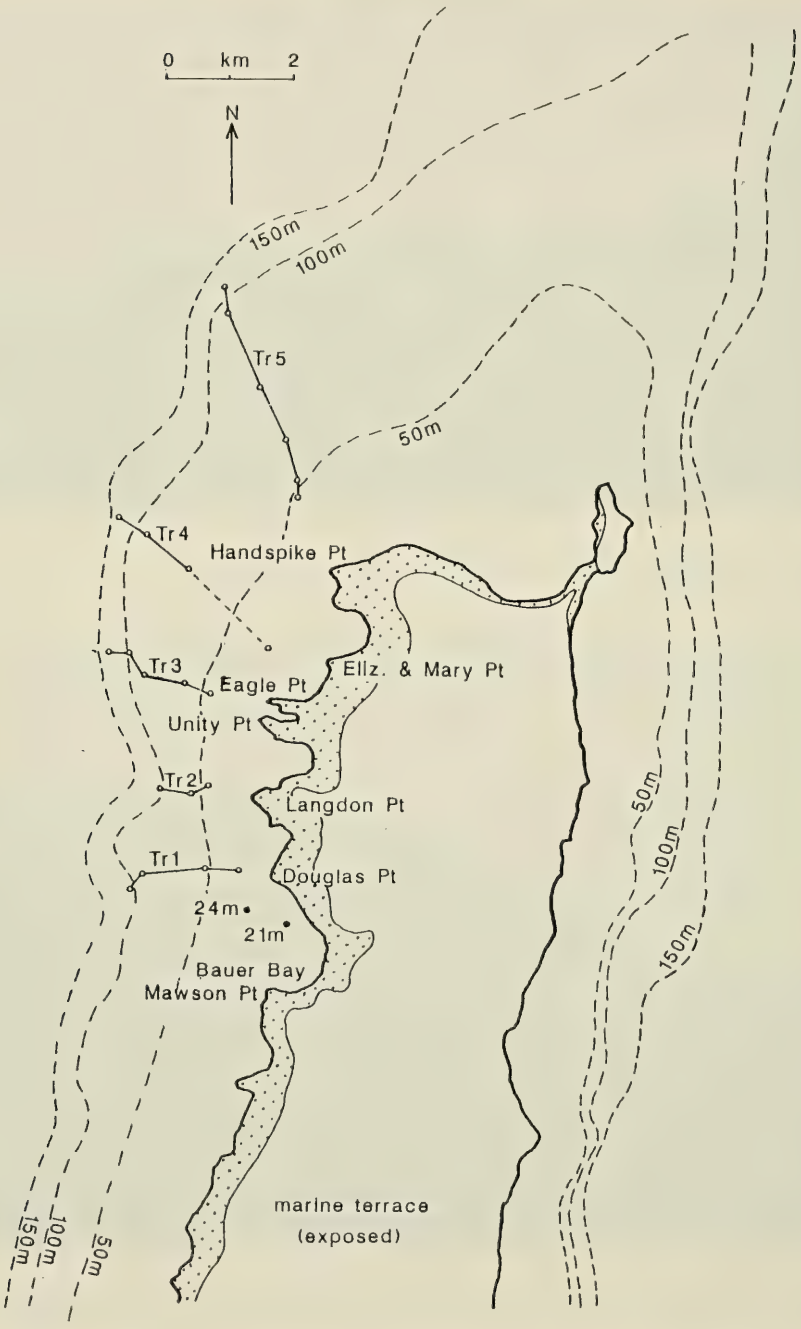

Fig. 6. Location of five LARC traverses, and approximate location of 50, 100 and 150m ocean depth contours around Macquarie Island. Marine terrace above present sea-level is stippled. Ocean soundings used to draw contours were obtained from an unpublished National Mapping compilation of soundings to 1970 and from MV 'Cape Pillar' soundings 1977, both charts held at the Australian Navy Hydrographic Office, North Sydney, NSW.

plotted are somewhat in error due to the difficulty of sighting accurately on a small craft in the heavy swell off the west coast, and the acknowledged shortcomings of the published 1:50 000 topographic map of the island used as the base for our maps (Berkery and Pritchard, 1987; Division of National Mapping, 1971). The errors do not affect the overall picture obtained.

Profiles along the traverses (Fig. 7) have been constructed, using a combination of these new data and that from the manuscript bathymetry charts. They show that the terrace slopes gently offshore to the west and north-west for between 1400 and 4600m. A distinct change of slope, at between 70 and 100m depth, marks the present seaward edge of the terrace. These measurements allow calculation of an overall slope of between 1 and 4° for the undersea part of the terrace (Table 1), comparing satisfactorily with Adamson, Selkirk and Colhoun's (1988) measured 1.5 to 4° slope for the onshore part of the terrace north of Bauer Bay.

Discussion

Profiles drawn across the northern part of the island from existing maps and data collected during the LARC traverses reported here show that the island is flanked to the west by a gently sloping platform at present partly above and partly below sea-level (Fig. 1, 3). The overall slope of the platform (1 to 4°), its total width (2000 to 5500m) and the depth of its westward margin below present sea-level (70 to 100m) are all consistent with predictions from the model proposed for formation of the raised marine platform (Adamson, Selkirk and Colhoun, 1988). This model is based on the known world-wide rise in sea-level following the last glacial maximum at c.18 000 years ago, and on tectonic uplift of the island. Between c.16 000 and c.8000 years ago sea-level appears to have risen faster than tectonic uplift so that wave action caused vigorous erosion of the coastal cliffs, leaving a sloping platform as rising sea-level allowed waves to reach successively higher parts of the coast, and causing cliff retreat equalling the width of the platform, (Fig. 9).

The maximum depth of the seaward edge of the submerged marine terrace is about 70 to 100m below present sea-level. The height of the landward edge of the exposed terrace is 15 to 20m above present sea-level, making a total height difference between seaward and landward edges of between 90 and 120m. This lies within estimates of global sea-level rise following the last glacial maximum period, and is consistent with our inference that the whole terrace formed during this period of rapidly rising sea-level.

Palaeolake deposits at the top of these cliffs (Fig. 8) are remnants of lakes which formerly occupied parts of the plateau lost during cliff retreat and terrace formation (Fig. 9). The ages of the uppermost layers of these deposits represent the approximate date of lake drainage, and provide an independent means of dating the formation of the cliff line between the terrace and the western plateau margin. Dates of 8620 ± 170 radiocarbon years (calibrated to 9420 ± 320 BP; Beta-20166) for a layer 220cm below the present surface vegetation at Palaeolake Skua, and of 5220 ± 80 radiocarbon years (calibrated to 6025 ± 290 BP; Beta-20164) for a layer 160cm below the present surface vegetation at Palaeolake Sandell (Selkirk *et al.*, 1988) are consistent with our interpretation that the cliff line had retreated to its present position by about 6000 years ago.

The erosive effectiveness of wave action on sea cliffs depends on wave size and energy, coastal seafloor morphology, and cliff lithology and structure. Macquarie Island lies in the latitudinal zone of maximal occurrence of gale force winds throughout the year in the Southern Hemisphere (Davies, 1980), and just to the east of the zone of maximum high-latitude cyclogenesis (Adamson, Whetton and Selkirk, 1988). This storm belt of the Southern Ocean is probably the most important area in the world for generating

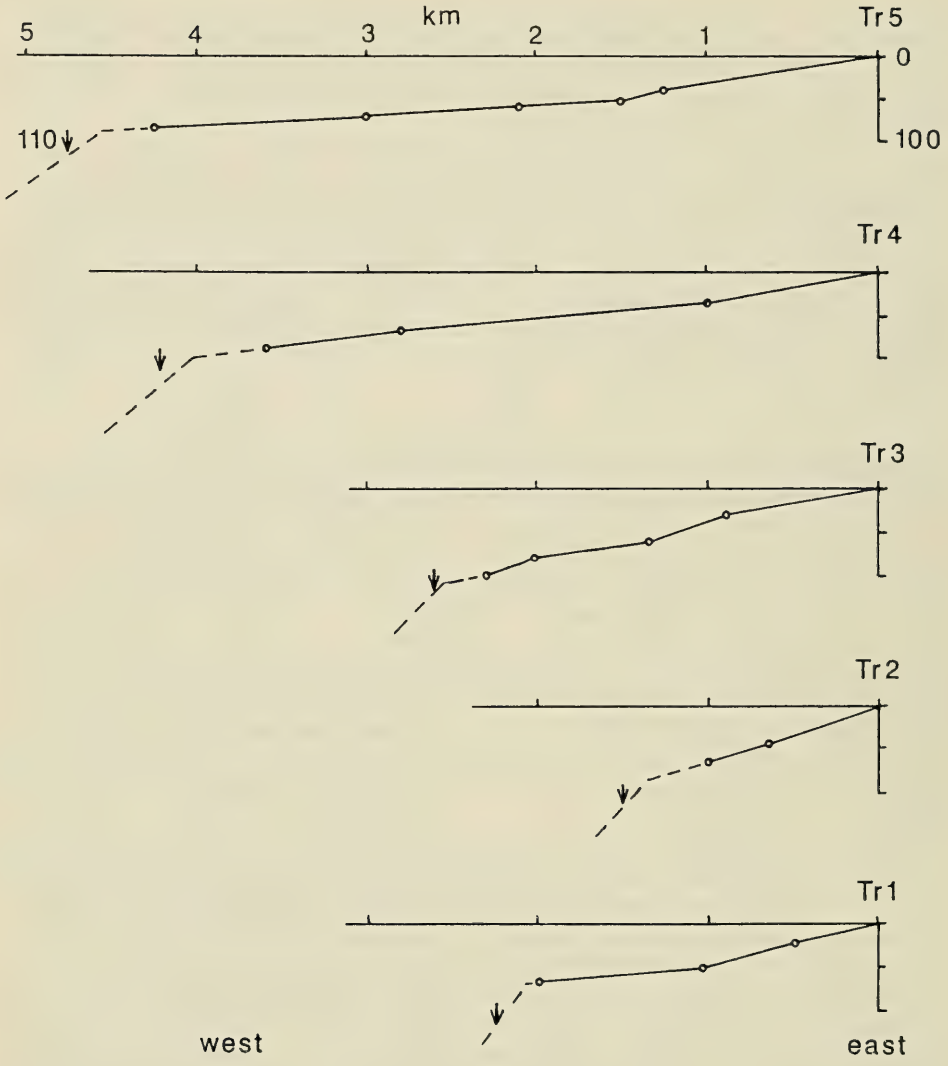

Fig. 7. Ocean depth along five LARC traverses off north-west coast of Macquarie Island. Location of traverses shown on Fig. 6. Open circles: spot depths from LARC. Arrow: depth measured from LARC greater than 110m (limit of depth sounder). Dashed line shows inferred break of slope at seaward edge of marine terrace.

swell and storm waves (Davies, 1980). At present on Macquarie Island there are about 6 days per month when average daily wind speed is gale force (17.5m s^{-1}) or above (Streten, 1988). Winds of these speeds generate large waves (Dackombe and Gardiner, 1983) of great energy (Davies, 1980). For the last 1 million years or so the belt of sub-tropical high pressure cells has been in its present position over about 30°S, and a westerly circulation has influenced Southern Australia (Bowler, 1982) and the Southern Ocean. To the north of Macquarie Island, in south-eastern Australia, between 18 000 and 16 000 BP major water deficit was accompanied by maximum aeolian activity (Bowler, 1982). To the south, in Antarctica, high particulate concentrations of continen-

tal dust derived from mid-lower latitudes are preserved in ice of last glacial maximum age indicating windy, vigorous atmospheric circulation globally and more aridity (De Angelis, Barkov and Petrov, 1987). It is clear that, between 16 000 and 8000 BP, approximately westerly winds no less strong than those of the present produced high energy waves which assailed the west and north coast of Macquarie Island.

Fig. 8. Bedded lacustrine deposits of Palaeolake Skua exposed in cliff at plateau edge about 180m a.s.l. Intermediate width marine terrace borders Sellick Bay on left of photograph.

Swell has strong erosive action where the coast is fronted by a platform shallow enough to steepen the wave form and generate breaking waves very close to or at the shore (Davies, 1980). Cliffs that plunge into deep water do not generate such erosive waves and, at the other extreme, an extremely shallow gently sloping platform causes energy dissipation after the waves have broken offshore. During formation of the Macquarie Island platform, when the sea was eroding the base of the cliffs and steep edges of the plateau, the gently sloping platform was below mean sea-level, and most of its width would have been below the level of effective wave abrasion (King, 1972). Much of the wave energy would have been delivered to erode the base of the cliffs and steep slopes of the western edge of the plateau. With a combination of swell, breaking because of the shelving platform, and storm waves from the presumably still frequent gales, the assailing force of waves on the island must have been high.

The resistance of cliff material to the erosive force of wave action is controlled by its lithology. The mechanical strength of cliff material is reduced by jointing, faulting and weathering (Sunamura, 1983), which are common features of Macquarie Island rocks. Macquarie Island is formed from igneous rocks, intrusive in the northern third, extrusive in the southern two thirds (Duncan and Varne, 1988). Sunamura (1983) compiled over 100 observations of rates of coastal cliff erosion from around the world. Rates ranged from about 1mm to several metres per year, depending on the resistance of the cliff material. Taking into consideration the fractured nature of much of the rock

(reducing its resisting force) and the high assailing force of the waves at Macquarie Island, an average rate of coastal cliff erosion of 0.5m per year during the period of rapid sea-level rise between 18 000 and 8000 years ago is quite possible.

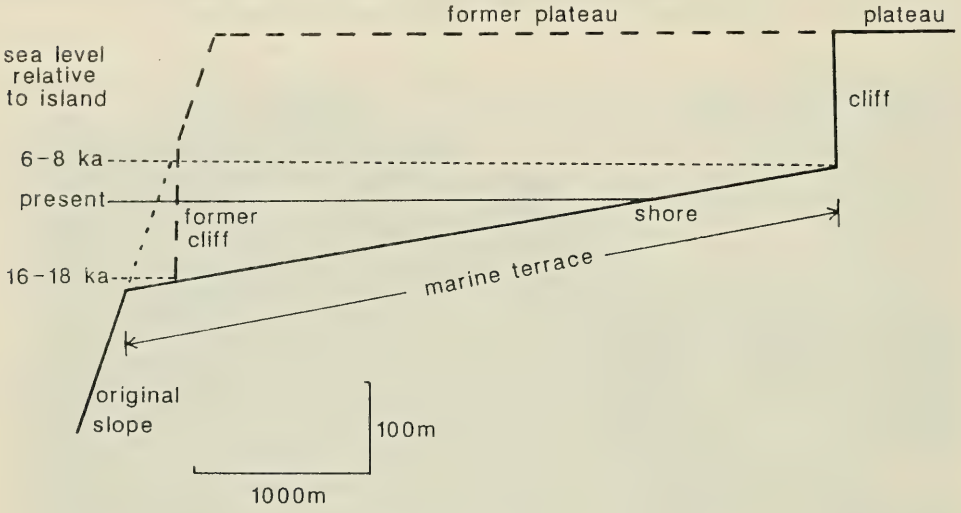

Fig. 9. Diagram to show formation of the wide marine terrace along the north-west coast of Macquarie Island since the last world-wide period of low sea-level about 18 000 years ago (18kA, last glacial maximum). The slope of the marine terrace approximates the minimum slope of a wave-cut rock surface in the Southern Ocean. An arbitrary original slope (probably fault-controlled) is assumed for the western side of the island block. The maximum depth (d) of wave erosion is presumed constant during terrace formation. Sea-level relative to the island is presumed to have changed throughout the last 18 000 years due to known rise in world sea-level (18 000 to 6000 years ago, 18-6kA) and presumed tectonic uplift (18 000 years ago to present, 18-OkA). Sea-level has remained at its present absolute level for about the last 6000 years (6kA). Diagram adapted from Fig. 21.2 of King (1972).

At present on the north-west coast of Macquarie Island, much of the wave energy from the Southern Ocean swell is dissipated offshore on the tectonically emerging gently sloping platform of bedrock and boulders so that wave action on the present shoreline is reduced relative to when the platform was being formed.

The west-north-west dominant orientation of wind, and the half-heart shape of Bauer Bay between Douglas Point and Mawson Point ensure that sand, carried down into shallow Bauer Bay by two major creeks from the plateau, will remain largely trapped there (Fig. 3). The orientation of shore and wind is also favourable for long-shore movement of sand at least south of Douglas Point. The extensive sand deposits at between 100 and 200m above present sea-level on the plateau above Bauer Bay (Adamson, Selkirk and Colhoun, 1988) suggest that sand has been trapped in former equivalents of the present bay during uplift of the island. The cobbled beach (Beach 5 of Ledingham and Peterson, 1984) is presumed to be approximately coeval.

The marine terrace, especially around the north-west coast, seems to be an unusually wide example of a Type A platform (King, 1972) with a gentle slope seaward, and little or no scarp formed by present wave action. The ultimate seaward scarp of this platform at about 70-100m below present sea-level was probably controlled by faulting and the lowest level reached by the sea at last glacial maximum time, c.18 000 BP. In Scotland raised coastal platforms and fossil sea cliffs of similar morphology have been formed by isostatic uplift after ice retreat (Steers, 1973).

The width of the marine terrace on the north-west coast far exceeds that formed by tidal action on a stable coast. By invoking the global rise in sea-level after the terminal Pleistocene glacial period, the extraordinary force of the Southern Ocean, the fractured nature of the rock, and an appropriate depth of water offshore, the width of the terrace can be explained. Tectonic uplift of the island probably occurred throughout the period of global sea-level rise. Continuing tectonic uplift of the island explains the present emergence of the landward portion of the terrace.

Differential tectonic movement of fault-bounded blocks, tilting of blocks, and more vigorous wave attack on the west coast may explain the great differences in width of emergent marine terraces around the coast (Fig. 1). The narrow or non-existent terrace along the east coast, in contrast to the wide western terrace, may be due to slight tilting of the northern half of the island downwards to the east. A shallow underwater platform is present off the east coast (Fig. 6).

The model originally proposed for the formation of the Macquarie Island marine terrace on the north-west coast (Adamson, Selkirk and Colhoun, 1988) is supported by bathymetric measurements. An assumed 8000 years of vigorous terrace formation (16 000 to 8000 years ago) has cut a terrace of total width 3700m and 2° slope (mean of 5 measured traverses). The landward edge of the terrace is estimated now to be at an altitude of 15 to 20m. Assuming this to have been raised from sea-level by tectonic activity during the past 6000 years of stable sea-level yields a calculated uplift rate of approximately 3mm per year. This value accords well with the independent estimates of Colhoun and Goede (1973), Bergstrom (1985) and Selkirk, Seppelt and Selkirk (1990) for the northern portion of the island between Green Gorge and the Isthmus.

Acknowledgements

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Review of the Discovery and Identification of Onychophora in Australia

N. N. TAIT, R. J. STUTCHBURY and D. A. BRISCOE

TAIT, N. N., STUTCHBURY, R. J. & BRISCOE, D. A. Review of the discovery and identification of Onychophora in Australia. *Proc. Linn. Soc. N.S.W.* 112 (2), 1990: 153-171.

Over one hundred years have elapsed since the first discovery of onychophorans in Australia. During that time six species were described, amidst considerable debate and controversy. More recent detailed morphological analyses have added two further species. However, we have recently applied molecular taxonomic techniques to the endemic fauna and identified over fifty previously unknown biological species. This review records the history of discovery of onychophorans in Australia as a basis for further studies.

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INTRODUCTION

Species delineation and reconstruction of phylogenetic relationships are particularly difficult in groups of organisms which are morphologically conservative and where the numbers of individual specimens available for examination are low. In these cases it is often impossible to determine whether subtle variations in morphological characters are the products of intraspecific variation, or evidence for the existence of more than one species. However, morphological conservatism does not necessarily reflect lack of diversity in other biological attributes such as polynucleotide sequences, protein structures and physiology. Over the last decade taxonomists have turned increasingly to the techniques of molecular genetics to provide independent data to resolve some of the more difficult problems.

Among the invertebrate phyla the Onychophora are considered to be an extremely conservative taxon, with limited morphological differentiation amongst members of the extant fauna. Moreover, comparisons of current forms with the scanty, but ancient, fossil record display striking similarities. Fewer than 100 species are recognized within the phylum world-wide, with eight species belonging to seven genera in Australia (Ruhberg, 1985; Ruhberg *et al.*, 1988). Recently, we have begun applying molecular taxonomic techniques to the Australian Onychophora and revealed an unsuspected extensive diversity of over fifty distinct species (Tait and Briscoe, 1990). These findings have led us to review the existing literature on endemic onychophorans and to present here a history of that knowledge as a base for subsequent taxonomic publications. This history includes not only some unusual onychophorans, but also some of the more colourful characters of Australian zoology.

ONYCHOPHORAN RELATIONSHIPS

Members of this phylum are commonly known as peripatus, after the first genus described (Guilding, 1826), or velvet worms, in reference to the texture of their integument. They have been allocated to two exclusive categories as 'missing links' and 'living fossils' (Hill, 1950; Ghiselin, 1984). Although they were first included with the molluscs (Guilding, 1826), their curious combination of annelid and arthropod characteristics were soon appreciated (Macleay, 1829; Gervais, 1837). However, their arthropod

features were subsequently ignored by many authors including Grube (1853) who created the order Onychophora to contain peripatus within the annelids. Their arthropod affinities were clearly established with a more detailed account of their internal anatomy and especially the discovery of their, albeit primitive, tracheal respiratory system (Moseley, 1874). Indeed, the Onychophora were seen to correspond with the Protracheata, a hypothetical ancestral group of the terrestrial arthropods, proposed earlier by Haeckel (1870, cited in Moseley, 1874).

The phylogenetic significance of the Onychophora has not diminished despite the recent controversy regarding the origins of, and relationships among, the various groups of extant arthropods. The monophyletic view is that the large number of synapomorphies displayed by all arthropods cannot be explained by convergent evolution (Clarke, 1979; Boudreaux, 1979; Mangum *et al.*, 1985; Wright and Luke, 1989), and the Onychophora are considered to be a sister group to the Euarthropoda within the phylum Arthropoda (Ax, 1984; Wright and Luke, 1989). In contrast, evidence from comparative functional morphology and embryology may be interpreted to indicate a polyphyletic origin of the arthropods and hence elevation of the Uniramia, Crustacea and Chelicerata to phylum rank (for review see Manton and Anderson, 1979). In this reassessment, the Onychophora represent a key position in the evolution of the essentially terrestrial uniramians. Sperm ultrastructural studies have also provided evidence for a phylogeny linking the clitellate annelids with the Onychophora and the other uniramians (Jamieson, 1986; 1987). Until this controversy is resolved, perhaps by the use of molecular taxonomic techniques (see Field *et al.*, 1988), most texts adopt the impartial view and designate the Onychophora as a discrete protostome phylum. The fossil record of onychophorans is sparse, and interpretation of its earlier members somewhat controversial. Fossils approaching present day onychophorans in general lobopodial body organization have been identified as *Xenusion anerswaldae* from the Early Cambrian Baltic (Pompeckj, 1927; Jaeger and Martinsson, 1967; Krumbiegel *et al.*, 1980); *Aysheaia pedunculata* from the Middle Cambrian Burgess Shale of British Columbia (Walcott, 1911; Whittington, 1978) and *A. prolata* from the Middle Cambrian Wheeler Formation of Utah (Robison, 1985). It has been suggested that these fossils be included as a taxon, Xenusia, of equal rank to the Onychophora and Tardigrada (Dzik and Krumbiegel, 1989).

Fossils with less contentious onychophoran affinities include *Helenodora inopinata* from the Late Carboniferous Mazon Creek beds of Illinois (Thompson and Jones, 1980) and in the rich assembly of the Late Carboniferous Montceau-les-Mines in central France (Heyler and Poplin, 1988). Both these fossil localities contain terrestrial and aquatic plants and animals, and so may represent the earliest record of terrestrial onychophorans. As yet, no fossil onychophorans have been identified from land masses where they presently exist.

The present day zoogeography of onychophorans is essentially one of Gondwanan origins, from tropical to Southern Hemisphere cool temperate regions (Brinck, 1956). They are divided into two families, the Peripatidae (Evans, 1901a) from tropical regions of West Africa, South-east Asia and central and South America and the Peripatopsidae (Bouvier, 1907) from South Africa, Australasia and Chile. Since both families are represented in Africa and South America, it would appear that the two families diverged before the break-up of Gondwana some 130 million years ago (Ghiselin, 1985).

Body organization and way of life are essentially similar in the one hundred or so extant species. Their inability to control water loss (Manton and Heatley, 1937; Manton and Ramsay, 1937; Morrison, 1946; Dodds and Ewer, 1952) confines them to terrestrial microhabitats of high humidity in rotting logs, under logs and stones, leaf litter and soil. They are negatively phototaxic (Holliday, 1942; Manton, 1938a; Brinck, 1956), forage

at night (Read and Hughes, 1987) and, in the laboratory, maintain a nocturnal activity rhythm (Alexander, 1957; Newlands and Ruhberg, 1978). They are active predators enmeshing their prey in jets of sticky slime ejected from a pair of modified limbs, the oral papillae, located on either side of the head. The prey is then torn open by the mandibles and immobilization completed by injection of saliva, which may also partially digest the flesh prior to it being sucked back into the mouth (Read and Hughes, 1987).

However, in their reproductive biology the Onychophora display great diversity. Female reproductive strategies span the spectrum from oviparity with yolky shelled eggs (Dendy, 1902); to ovoviviparity with yolky eggs (Sheldon, 1888; Evans, 1901b; Anderson, 1966); to viviparity with yolk-free eggs (Manton, 1949) and placental viviparity (Anderson and Manton, 1972).

Males generally produce spermatophores (Storch and Ruhberg, 1977). In species of *Peripatopsis* spermatophores may be deposited on any part of the body of the female (Sedgwick, 1885; Manton, 1938a; Ruhberg, 1985). Invading haemocytes bring about the destruction of the cuticle and the spermatophore envelope at their point of contact and the spermatozoa travel through the haemocoel to the ovary which they penetrate to reach the lumen (Manton 1938b). In contrast, spermatophores of the genus *Peripatus* are reported to be implanted directly into the female genital opening (Lavallard and Campiglia, 1975; Schaller, 1979). In the genus *Paraperipatus*, males lack the ability to produce spermatophores (Willey, 1898; Cuénot, 1949) and insemination is presumably direct (Schaller, 1979).

The recent discovery of a number of previously undescribed Australian onychophorans, with male head structures involved in sperm transfer, indicates that male reproductive biology may be as diverse as that of their female counterparts (Tait and Briscoe, 1989; 1990).

Historical Review and Discussion

Early Records

The first scientific record of an Australian onychophoran was made by Rudolf Leuckart, then Associate Professor of Zoology at the University of Giessen. In his report of the scientific achievements in the natural history of lower animals for 1860, he recorded that he could add to the list of known species of *Peripatus*, a new one from Australia, which (incorrectly) was distinguished by possessing sixteen pairs of legs (Leuckart, 1862).

The specimen was subsequently passed on to Mr H. Saenger, who included a short description of it, as *Peripatus Leuckartii* (Saenger, 1869). Subsequent changes in spelling and synonomies are given in Table 1. Saenger's account gave a marginally more precise locality 'north-west of Sydney' and established the correct number of walking legs (15 pairs), but the reported lack of claws on the first pair was later to provide confusion. Saenger's paper (1869) was reviewed by Leuckart in his reports for the years 1868-69 and 1870-71 (Leuckart, 1869; 1871).

Almost twenty years elapsed after Leuckart's (1862) note before Australian peripatus were again mentioned in the scientific literature. In 1886 two specimens from Cardwell in North Queensland were sent to Mr Henry Tryon of the Queensland Museum (Tryon, 1887), subsequently exhibited in Sydney in November 1886, and then lost. Tryon next met with peripatus under dead wood in a gully in Victoria Park, Brisbane, and, accompanied by Mr Frederick Skuse, under stones close to the Brisbane General Hospital. These specimens were exhibited to the Royal Society of Queensland on 15 April, 1887 (Tryon, 1887). This rediscovery of peripatus in Australia created such

interest that it was reported the next day in the 'Brisbane Courier' of Saturday, 16th April, 1887, where a half column was devoted to a very scientific discussion of its biology and significance.

In the same year, Professor Jeffrey Bell, of King's College, London, and the British Museum of Natural History, published a notification of two specimens sent to him by Dr. Edward Ramsay, Curator of the Australian Museum, Sydney, and collected in the 'Queensland Scrubs' near Wide Bay (Bell, 1887). The specimens were forwarded to Adam Sedgwick, of the University of Cambridge, and an account of them was incorporated into his monograph on the genus *Peripatus* (Sedgwick, 1888). Skuse (1897) later claimed that the specimens referred to by Sedgwick as coming from Wide Bay were in fact collected, by him, under stones close to the Brisbane General Hospital and Acclimatisation Society's Grounds on 3rd April, 1887, presumably on his outing with Tryon.

1887 also marked the first in a series of papers on peripatus by Mr. Joseph James Fletcher, the newly appointed director and librarian of the Linnean Society of New South Wales. This was a note and exhibition of a specimen with 15 pairs of claw-bearing legs obtained from Warragul in Victoria (Fletcher, 1887). No comparison was made with the Queensland specimens but Fletcher considered it of sufficient interest as a record of the wide distribution of peripatus in eastern Australia. Following the discovery of peripatus in Queensland and Victoria, an accurate locality in New South Wales was provided by the exhibition of a specimen from Cassilis (Olliff, 1887).

In the Australasian section of his 1888 monograph, Sedgwick included a description of *P. novae-zealandiae* (Hutton 1876) and *P. leuckartii* which he based on the two specimens from Wide Bay (or, according to Skuse (1897), from Brisbane) Queensland. The diagnosis of *P. leuckartii* was: Australian peripatus with fifteen pairs of legs, an accessory tooth on the outer blade of the jaw (absent in *P. novae-zealandiae*) and a white papilla on the ventral side of each of the last pair of legs in the male (absent in *P. novae-zealandiae*). Sedgwick also noted that the genital pore of the female *P. leuckartii* — was situated on the tip of a conspicuous protuberance. This feature, an ovipositor, was later to assume importance in indicating an oviparous mode of reproduction.

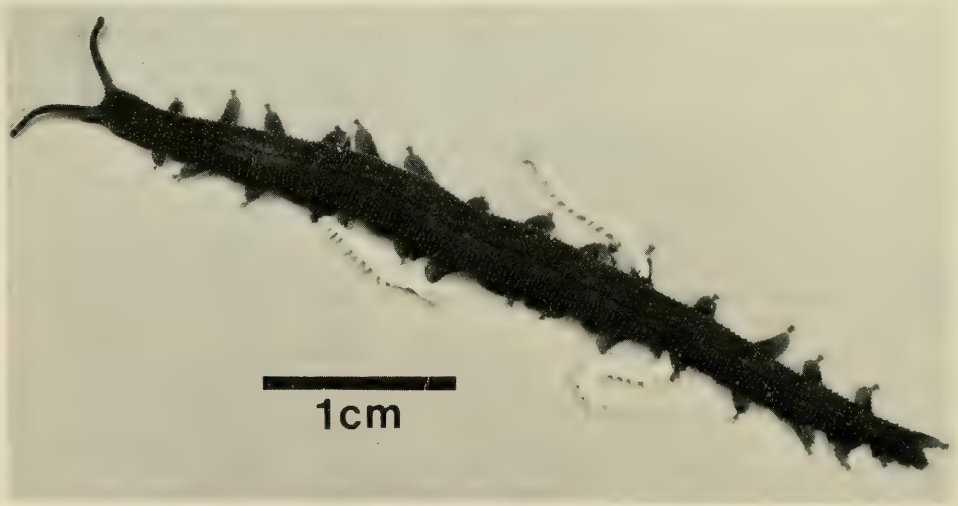

Fig. 1. Female and new born young of the ovoviviparous *Euperipatoides leuckartii*, the first species of an onychophoran described from Australia.

Fletcher's enthusiasm for onychophorans apparently increased during 1888, as evidenced by his presentation of three exhibitions. The first, on 27th June, noted that specimens collected near Wollongong were of a prevailing dull black or brown and red colouration, in contrast to the indigo-blue of those from Queensland, and foot-noted that dissection of one individual showed it to be pregnant (Fletcher, 1888a). Later, on 31st October, he exhibited the four newly-born progeny of one of his June specimens and noted their size (7mm when extended) and colouration (almost colourless to conspicuous pigmentation within a few days) (Fletcher, 1888b); see Fig. 1. On November 2nd, he exhibited, and noted the colour variation between, two specimens from Burrawang, near Moss Vale in New South Wales (Fletcher, 1888c).

The known range of peripatus in New South Wales was extended over the next few years with Fletcher's receipt of specimens from Dunoon (on the Richmond River in the north), the Blue Mountains and, most surprisingly, from the Mount Kosciusko region (southern alps) (Fletcher, 1890). The last were collected by Mr. R. Helms in March 1889 at Pretty Point and Wilson's Valley at altitudes of over 1500 metres where, for some months of the year, the ground is frequently covered with over a metre of snow (Helms, 1890). Fletcher (1890) described the variation in colour of the specimens from each of the three localities. The prevalent colours were indigo-blue and red, either of which could predominate, with longitudinal stripes of light and dark colour most conspicuous in specimens with a maximum of red.

Before the turn of the century, predominantly dry inland onychophoran localities at Tamworth (Paulden, 1898) and Moree in the north-western plains (Waite, 1895), were added to Olliff's (1887) Cassilis record.

Meanwhile Arthur Dendy, of the University of Melbourne, had described two specimens collected at Warburton in Victoria (Dendy, 1889a; b); Dendy often published the same article simultaneously in a local and an overseas journal. Although possessing fifteen pairs of claw-bearing legs, they were so strikingly different from both *P. leuckartii* and *P. novae-zealandiae* in colour and pattern that Dendy considered that they belonged to a separate species.

Sedgwick lost no time in refuting Dendy's assumption that a new species designation was warranted (Sedgwick, 1889). He pointed out that specimens he had examined from both New South Wales (donated by Mr Olliff) and Queensland were identical and, therefore, he doubted the distinctiveness of any Victorian forms. Furthermore, the considerable colour variation exhibited within both *P. capensis* (Grube 1866) and *P. novae-zealandiae* indicated the danger of using colour in species identification. In a personal letter Fletcher also cautioned Dendy regarding the use of colour in species identification (Dendy, 1889c).

These communications seem to have had the desired effect. In his next article, Dendy described the colour variation in eleven specimens of peripatus collected near Ballarat, Victoria (Dendy, 1889c). The external features used in the diagnosis of *P. leuckartii* by Sedgwick were shared with the Victorian specimens. Thus Dendy was persuaded to accept only one species of peripatus so far described from Australia. In the handbook provided for the use of members of the Australasian Association for the Advancement of Science (AAAS) held in Melbourne in 1890, Dendy noted the significance of peripatus and the occurrence of *P. leuckartii* in Victoria (Dendy, 1890a).

A turning point came in 1890 with the description of a new species, *P. insignis*, from Macedon, Victoria (Dendy, 1890 b,c). This form was distinguished from *P. leuckartii* in possessing only 14 pairs of legs, and the absence of the accessory tooth on the outer blades of the jaw and the white papillae on the bases of the last pair of legs of males. The

female genital aperture was located at the tip of a prominent white protuberance (later termed an ovipositor).

The known distribution of peripatus was extended to include Tasmania in a note on the existence of a bleached specimen, possessing fifteen pairs of legs, in the Macleay Museum at the University of Sydney (Fletcher, 1890). Except for the locality being Tasmania, no other information accompanied the specimen, which no longer exists in the museum (Horning, 1989, pers. comm.). This is regrettable as the specimen raises an intriguing historical possibility. In his letter of 1829, William Sharp Macleay (Macleay, 1829) comments that there is a specimen of peripatus in the collection of his father, Alexander Macleay. If this specimen corresponded to the one viewed by Fletcher, it would represent the first Australian onychophoran, predating Leuckart by nearly 40 years.

In 1895 Professor Baldwin Spencer, of the University of Melbourne, collected specimens which he identified as *P. insignis*, at Dee Bridge, Tasmania (Spencer, 1895). He did, however, note the relatively large size of these individuals, in comparison to Victorian forms of *P. insignis*. This distinction later led Cockerell (1913) to name the Tasmanian peripatus after Spencer (Table 1). Flynn (1918) added further localities at Great Lake and near Hobart.

The year 1895 was also notable for the first collection from Western Australia. Five specimens from Bridgetown had fifteen pairs of legs but lacked an accessory tooth on the outer blades of the jaws (Fletcher, 1895). Were these animals a variety of *P. insignis* with an additional pair of legs, or *P. leuckartii* without an accessory tooth? They were to play an important part in an acrimonious dispute on the taxonomy and reproductive biology of peripatus which had developed between Fletcher and Dendy.

Viviparity, Oviparity and Taxonomy

Apart from Fletcher's observation of the sudden appearance in vivaria of juveniles (Fletcher, 1888b), nothing was known of the reproductive biology of the Australian species. Fletcher assumed that the young were born alive as viviparity had been described in various species of peripatus from other continents.

In May, 1891, Dendy obtained several specimens, with fifteen pairs of legs, and hence referable to *P. leuckartii*, from Macedon, Victoria, the type locality of *P. insignis*. One male and three females were maintained in a vivarium for long-term observation and on 31st July, several eggs were found deposited beneath and in the crevices of bits of rotten wood (Dendy, 1891a,b,c,d). The identity of the eggs was in no doubt as dissection of the genital tract of females revealed eggs of comparable form; very large, oval, and each enclosed in a very tough, thick membrane. In the eggs from dissected females this membrane appeared smooth, while in the deposited eggs it was exquisitely sculptured (Fig. 2). On the basis of these observations, Dendy concluded that *P. leuckartii*, as he had been persuaded to call the Victorian specimens with fifteen pairs of legs, was oviparous, that Fletcher's intimated conclusions regarding viviparity were in error, and that Fletcher had failed to notice laid eggs in his vivarium. Dendy expected the eggs to hatch in October, based on Fletcher's finding of juveniles in that month.

The response to this report of oviparity in Australian peripatus was immediate and critical. Sedgewick (1891) suggested that it was no more than a case of abnormal extrusion of undeveloped embryos induced by stress. This criticism entirely misrepresented Dendy's description of eggs with a thick shell, a development that does not occur in viviparous species.

Fletcher's criticism was even more overt (Fletcher, 1891a), stating that no matter what mode of reproduction occurred in peripatus from Victoria, those from New South Wales were definitely viviparous. He exhibited a series of twenty eight embryos

including individuals whose development was so nearly complete that they must have been close to parturition. He followed this by an exhibition of about one hundred specimens from the Blue Mountains, together with their progeny, prematurely-born young of an accidentally injured female, advanced embryos extruded during the drowning of their mothers, and dissected females showing the oviducts crammed with embryos (Fletcher, 1892a).

Fletcher elaborated a defense of his own conclusions and an attack on Dendy in a paper read to the Linnean Society of New South Wales on 27th April 1892 (Fletcher, 1892b). He appeared to be particularly incensed to read the claim (Dendy, 1891a,b,c,d) that '. . . hitherto little has been known of its habits and nothing of its mode of reproduction.' He tartly replied that he would have no difficulty in proving, even to Dendy's satisfaction, that the New South Wales peripatus was '. . . viviparous in 1888, that it is still viviparous in 1892, and that in the interval it was also viviparous . . .'! He pointed out that the first dissected specimen of *P. leuckartii* (Fletcher, 1888a) was full of advanced embryos similar to those found in South African *P. capensis* by Moseley (1874), and therefore in accordance with what was known of other species.

Fletcher was by no means convinced that Dendy's Victorian forms were oviparous, adding to the doubt already seeded by Sedgwick (1891). He stated that Dendy should have confined himself to Victorian peripatus and not generalized to include New South Wales forms. Nonetheless, he conceded, 'If the Victorian peripatus really is oviparous, then it is oviparous . . . also the mode of (its reproduction) will almost certainly differ from that of the New South Wales peripatus . . .'

Dendy replied to this criticism at the Hobart meeting of the AAAS (Dendy, 1892a) and provided further information to support his views (Dendy 1892b,c). First, he pointed out that it was Fletcher and Sedgwick who persuaded him that Victorian specimens should be referred to *P. leuckartii*. Second, Dendy was not aware of contradicting any statement regarding the mode of reproduction in the New South Wales form, for the simple reason that he could not find any definite statement for him to contradict. Dendy now fully admitted that he had been incorrect in his interpretation of the mode of reproduction in the New South Wales specimens but that he was, nevertheless, justified in his conclusions.

The solution to the whole difficulty was simple. Dendy's original opinion was correct and the Victorian form with fifteen pairs of legs was specifically distinct from *P. leuckartii*. He refrained, at the time, from giving it a name.

Meanwhile the catalysts of this acrimony, the eggs found on 31st July 1891 in Dendy's vivarium, had not hatched. One, dissected in October, surprisingly revealed no sign of an embryo but, by November, coiled embryos were evident within several eggs. Dissection of one of these revealed an advanced embryo. By April 1892 only three eggs remained. Nearly a year later, on January 3rd 1893, the one remaining egg was found to have split on one side and a young peripatus had emerged. Ironically, after seventeen months of patient vigilance, Dendy found it dead in the container (Dendy, 1893a,b). Although the eggs were maintained under artificial conditions, these observations indicated an extraordinarily long incubation period for this species and vindicated Dendy's proposition that Victorian peripatus were egg-layers. It would seem that the controversy should now have abated. This was not to be.

By this stage two named species were acknowledged in Australia, *P. leuckartii* and *P. insignis*, together with the unnamed Victorian oviparous form studied by Dendy. Even this meagre consensus was disturbed by Dendy in his presidential address to the biological section of the AAAS meeting in Brisbane in January, 1895. Dendy reported a recently acquired translation of Saenger's (1869) diagnosis of *P. leuckartii*, obtained from Professor Baldwin Spencer (Dendy 1895a). He suggested that the description more

closely fitted *P. insignis*. i.e. fourteen pairs of claw-bearing legs and the first, clawless legs were really the oral papillae.

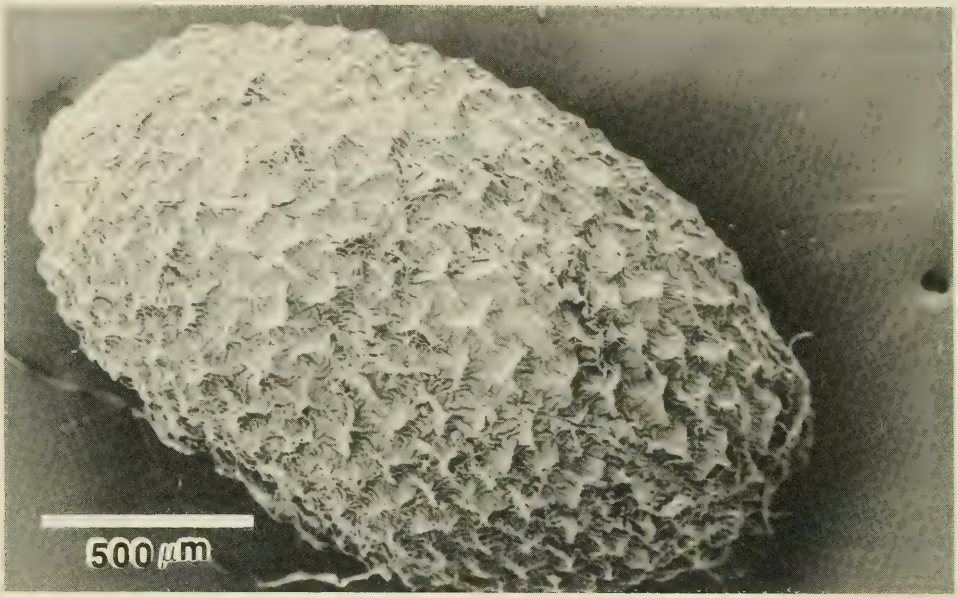

Fig. 2. Scanning electron micrograph of the sculptured egg of the oviparous *Ooperipatellus insignis*.

On his way to the meeting, Dendy had met with Fletcher in Sydney and discussed nomenclature (Dendy, 1902). They decided to each present a paper at the next meeting of the Linnean Society of New South Wales, Fletcher to confine himself to the viviparous form from New South Wales, and Dendy to the oviparous Victorian species. They agreed the latter should now be named. This arrangement did not last long. Fletcher received the specimens from Bridgetown, Western Australia which possessed fifteen pairs of legs (like *P. leuckartii*) but with the outer jaw blade morphology of *P. insignis*. The concept of erecting yet another species was too much for Fletcher, '. . . Australia would, I think, be oversupplied with as many as four species' (Fletcher, 1895).

Fletcher commented on variation in the form of the accessory tooth in the New South Wales specimens and that it would seem the number of legs was also variable (fourteen or fifteen pairs) especially as a New Zealand form with sixteen pairs of legs had recently been discovered and designated a subspecies *P. novae-zealandiae* (*suteri*) (Dendy, 1894a,b).

Thus Fletcher writes, 'The most satisfactory arrangement, in my opinion, would be to consider all the known Australian specimens of peripatus as referable to one comprehensive species with four varieties'. His species diagnosis is all encompassing, 'With fourteen or with fifteen pairs of claw-bearing, ambulatory legs; outer jaw blades without or with an accessory tooth, occasionally more, at the base of the main tooth; males smaller than females, with a pair of (accessory gland) pores close together and situated between the genital papilla and the anus; with a white or sometimes bluish tubercle, on which opens the crural gland, on each leg of the first pair only, or of the last pair only, or of all or only some of the pairs with the exception of the first, or of the first five.' The distribution was described as suitable situations in the tableland and coastal regions of

Queensland and New South Wales, Victoria, Tasmania, and Western Australia. The four varieties included:

i. *P. leuckarti* Saenger var. *typica* = *P. insignis*, Dendy. With fourteen pairs of claw-bearing legs; outer jaw blades without an accessory tooth. New South Wales, Victoria and Tasmania.

ii. *P. leuckarti* Saenger var. *occidentalis, var. nov.* With fifteen pairs of walking legs; outer jaw blades without an accessory tooth. Bridgetown inland from Perth, Western Australia.

iii. *P. leuckarti* Saenger var. *orientalis, var. nov.* With fifteen pairs of walking legs; outer jaw blades with one or several accessory teeth. Queensland and New South Wales.

iv. The Victorian *Peripatus* to be dealt with by Dr. Dendy. Victoria and Tasmania (probably for the bleached specimen in the Macleay Museum).

Thus Fletcher had taken up Dendy's tentative suggestion that *P. insignis* was the real '*leuckartii*' without reference to the type specimen.

From Fletcher's descriptions of the various subspecies of *P. leuckartii*, some indication of morphological differentiation is evident in the distribution of the crural glands in males. The extraordinary range outlined in the species diagnosis does not occur in each of the subspecies. Thus *P. leuckarti typica* has crural glands on all legs except the first five pairs, while in *P. leuckarti occidentalis* they are present on all legs except the first pair. *Peripatus leuckarti orientalis* is unusual in that while most individuals have a similar distribution of crural glands to *P. leuckarti occidentalis* some have a distinctive pattern with crural glands on the first pair of legs only. The first record of an individual with this .pattern was for a specimen collected in the Blue Mountains (Fletcher, 1891b). Subsequently as many as thirty individuals had been identified displaying this distribution of crural glands. It is evident that Fletcher's view of how many species of peripatus Australia could support prevented him from diagnosing specific differences and indeed in one subspecies, *P. leuckarti orientalis*, he could in fact have incorporated two species each displaying a distinctive pattern of crural glands in the males. The distribution of crural glands was later to receive prominence in the identification of Australian onychophorans (Ruhberg, 1985; Ruhberg *et al.*, 1988).

Apart from a short note on the extension of the distribution of a New Zealand species (Fletcher, 1900), this was to be Fletcher's last word on the subject of peripatus taxonomy.

Dendy's paper, confined as agreed to the Victorian egg-laying species with fifteen pairs of legs, was published next to Fletcher's (Dendy, 1895b) and in an abridged form (Dendy, 1895c). Dendy was presumably unaware of what Fletcher had done to the taxonomy of Australian peripatus and he provided a detailed description of the reproductive anatomy of *P. oviparus n. sp.* with an account of the formation of the egg membranes. This was the first report to correlate the presence of a large extensible ovipositor between the last pair of legs in females with the oviparous mode of reproduction. No comment was made about the possibility of *P. insignis* being oviparous although this species had been described as possessing a conspicuous ovipositor (Dendy, 1890 b,c).

The distribution of oviparous species was soon extended to include New South Wales and Queensland. Already Sedgwick (1888), in his description of *P. leuckartii* from southern Queensland, had noted the presence of an ovipositor, but this was not taken at the time as an indication of oviparity. Thomas Steel, an industrial chemist with the Colonial Sugar Refining Company in Sydney and twice President of the Linnean Society of New South Wales, made the next contribution. He had reported extensively on the colour variations, behaviour and sexual biology of viviparous specimens from the Moss Vale District, New South Wales (Steel, 1896). In the following year (Steel, 1897),

he noted the possible occurrence of *P. oviparus* between Exeter and Bundanoon, in the same general area as Moss Vale, based on a specimen with striking colour and a fully extended ovipositor. Furthermore, Steel re-examined the specimens collected by Helms at Mount Kosciusko (Fletcher, 1890) and noted that they too had conspicuous ovipositors and were, in all probability, *P. oviparus*. Spencer (1892) collected nine peripatus near Cooran in southern Queensland. Subsequent examination of one female revealed an ovipositor (Dendy, 1902).

The range of oviparous onychophorans, unknown elsewhere in the world, soon included New Zealand. In 1900 Dendy reported a species, from the South Island, which had fourteen pairs of legs and a conspicuous ovipositor in females (Dendy, 1900a,b). He proposed the name *P. viridimaculatus*. During the same year Fletcher (1900) exhibited specimens from the North Island which he referred to as *P. viridimaculatus*.

The first attempt at generic re-evaluation of the rapidly accumulating species of *Peripatus* world-wide, was by Pocock (1894). He proposed three genera: *Peripatus* to be retained for neotropical species; *Peripatopsis* for South African species; and *Peripatoides* for those from Australia and New Zealand. This led to the erection of many new genera within each of these geographical areas.

By 1900 Dendy had amassed enough information to propose that the three species of oviparous peripatus should be given a separate generic designation (Dendy, 1900c). The genus *Ooperipatus* was proposed to include:

i. *O. oviparus*, with 15 pairs of legs and an accessory tooth on the outer blade of the jaw. Victoria, N.S.W. and Queensland.

ii. *O. insignis*, with 14 pairs of legs and no accessory tooth on the outer blade of the jaw. Victoria and Tasmania.

iii. *O. viridimaculatus*, with 14 pairs of legs, no accessory tooth on the outer blade of the jaw and distinctive colour pattern. North and South Islands of New Zealand.

While each of these species was characterized by the presence of a conspicuous ovipositor, shelled eggs had only been identified in *P. oviparus* and *P. viridimaculatus*. Specimens of *P. insignis*, so far collected, were small and contained neither eggs nor embryos.

Thus by the turn of the century, six species of peripatus had been described from Australia and New Zealand, three of which were distinguished by the egg-laying mode of reproduction. Although Sedgwick cautioned against the erection of new genera (Sedgwick, 1908), the *ad hoc* erection of genera continued and *Peripatoides* became entrenched to accommodate the viviparous species; *P. leuckartii* in the east and *P. occidentalis* (elevated to species rank by Bouvier (1907)) and the later identified *P. gilesii*, in the west with *P. novae-zealandiae* and *P. suteri* from New Zealand. The genus *Ooperipatus* was also retained to include the oviparous species; *O. oviparus* from Victoria, New South Wales and Queensland, *O. insignis* from Victoria and Tasmania and *O. viridimaculatus* from New Zealand (Dendy, 1900c).

Having been the prime instigator of the recognition of oviparity in some species of Onychophora, Dendy culminated his contribution with a detailed description of the three egg-laying species from Australia and New Zealand (Dendy, 1902). Although Dendy was responsible for initiating the idea that the Victorian species with fourteen pairs of legs (*O. insignis*) was possibly the real '*leuckartii*' (Dendy, 1895a), he had abandoned this notion in his revision of the generic designation of the oviparous species (Dendy, 1900c). Dendy's observations of Leuckart's specimen at the Leipzig Zoological Museum finally confirmed that it was identical to the ordinary viviparous form with fifteen pairs of legs found in New South Wales (Dendy, 1906). Hence it was left to Fletcher to perpetuate the notion, that the real '*leuckartii*' had fourteen pairs of legs, in his

view of the taxonomy of Australian peripatus as one comprehensive species with *O. insignis* designated *P. leuckarti typica* (Fletcher, 1895). Steel concluded his contribution with an account of peripatus in the first edition of the Australian Encyclopaedia (Steel, 1925).

Later Discoveries and Revisions

In 1905 the Hamburg expedition to Western Australia, led by Professor W. Michaelson and Dr. R. Hartmeyer, collected onychophoran specimens at Lion Mill in the Darling Ranges, inland from Perth. These were distinctive in possessing sixteen pairs of legs, but shared with *P. occidentalis* the absence of accessory teeth on the outer jaw blade. Bouvier (1909a,b) named these *Peripatoides Woodwardi*. Prior to the German expedition, Mr. H. M. Giles, of the Zoological Gardens in Perth, had made several collections (Woodward, 1906) and sent four animals, from Armadale, southeast of Perth, to Baldwin Spencer who described them as *P. gilesii* (Spencer, 1909). Professor William Dakin, of the University of Western Australia, while attempting to identify onychophorans from Mundaring Weir in the Darling Ranges, recognised the potential synonomy of *P. gilesii* and *P. woodwardi* from such close localities. Comparisons of his specimens with type specimens of Spencer and the descriptions of Bouvier (1909a,b) confirmed the synonomy. The name *P. gilesii* took precedence by less than nine months (Dakin, 1914a,b).

Furthermore, comparison of *P. occidentalis* with *P. gilesii* resulted in a surprising conclusion (Dakin, 1920). Apart from the number of legs, the two species agreed in all other respects. This included the distribution of the crural glands as occurring on all pairs of legs. Dakin settled the conflicting reports of the number of pairs of these structures in the Western Australian species (Fletcher, 1895; Bouvier, 1900; Haddon, 1913) by pointing out the difficulty in identifying crural papillae from external examination due to variation in their state of protrusion. Careful dissection is the only way to reveal the correct number of papillae and their associated glands. On this basis Dakin concluded that the two forms were varieties of one species. Since *P. occidentalis* had precedence over *P. gilesii*, the former was retained. Thus Dakin reduced the number of species of peripatus in Western Australia from three to one.

The contribution made by the eminent zoologist, Bouvier, to the biology of Onychophora extends far beyond his naming of Australian species. His work, and a synthesis of others, is embodied in two large monographs (Bouvier, 1905a, 1907). Bouvier divided the Onychophora into two families: the Peripatidae (Evans, 1901a) to include the tropical forms from Africa, South-east Asia and central and South America, and the Peripatopsidae (Bouvier, 1907) from South Africa, Australasia and Chile. In his first publication on Australasian onychophorans he commented on the paucity of specimens from the region, held in the British Museum, but, nonetheless, noted that the male of *P. leuckarti orientalis* possessed crural papillae on legs two to fifteen inclusive (Bouvier, 1900). The species designation was later changed to *Peripatus orientalis* (Bouvier, 1902) and then to *Peripatoides orientalis* in a more detailed account of its anatomy (Bouvier, 1905b). Bouvier's monograph (1905a) contained an unfortunate number of errors, largely emanating from the Dendy-Fletcher controversy, some of which were pointed out in an otherwise complimentary postscript to Dendy's (1906) paper.

While Bouvier accepted Dendy's genus *Ooperipatus* '. . . by a series of unfortunate misprints, this name is in many places confounded with the name *Eoperipatus* given by Mr Evans to a totally distinct genus' (Dendy, 1906). Even more confusing was the designation of a species in a figure legend as *Ooperipatus leuckartii*. Bouvier retained these misconceptions in his second monograph (Bouvier, 1907). *Peripatoides orientalis* (designated *Peripatus leuckarti orientalis*, Fletcher, 1895) should have been *P. leuckartii; Ooperipatus*

TABLE 1

Chronological sequence of identification and synonomies of species of Australian peripatus

Author (date)	Designated Generic Names with			
Leuckart (1862)	*Peripatus* sp.			
Saenger (1869	*Peripatus Leuckartii*			
Dendy (1889a,b)			*Peripatus* sp.	
Dendy (1889c)			*Peripatus leuckartii*	
Dendy (1890b,c)				*Peripatus insignis* Victoria)
Pocock (1894)	*Peripatoides* designated as genus for Australasian species with *Peripatoides noveazealandiae* specified as type species			
Spencer (1895)				*Peripatus insignis* (Tasmania)
Dendy (1895a)				*Peripatus leuckartii*
Fletcher (1895)	*Peripatus leuckarti orientalis*		*Peripatus leuckarti* s.sp	*Peripatus leuckarti typica*
Dendy (1895b)			*Peripatus oviparus*	
Dendy (1900c)			*Ooperipatus oviparus*	*Ooperipatus insignis*
Bouvier (1907)	*Peripatoides orientalis*		*Ooperipatus oviparus*	*Ooperipatus leuckarti* / *Ooperipatus insignis*
Spencer (1909)				
Bouvier (1909a,b)				
Cockerell (1913)			*Symperipatus oviparus*	*Ooperipatus insignis* / *Ooperipatus spenceri*
Dakin (1914a,b)				
Bouvier (1915)				
Dakin (1920)				
Hardie (1972)	*Peripatoides leuckartii*		*Peripatoides oviparus*	*Peripatoides insignis*
Bachr (1977)				
Ruhberg (1985)	*Euperipatoides leuckarti*	Euperipatoides sp.	*Ooperipatus oviparus*	*Ooperipatellus insignis*
Ruhberg *et al.* (1988)				

Specific Sub-specific Epithets					
	Peripatus leuckarti occidentalis				
	Peripatoides occidentalis				
		Peripatoides gilesii			
		Peripatoides Woodwardi			
		Peripatoides gilesii			
			Ooperipatus paradoxus		
	Peripatoides occidentalis occidentalis	*Peripatoides occidentalis gilesii*			
	Peripatoides occidentalis	*Peripatoides gilesii*			
Ooperipatus decoratus			*Austroperipatus paradoxus*		
	Occiperipatoides occidentalis	*Occiperipatoides gilesi*	*Austroperipatus paradoxus*	*Mantonipatus persiculus*	
					Cephalofovea tomahmontis

leuckartii (designated *Peripatus leuckarti typica* by Fletcher, 1895) should have been *Ooperipatus insignis* (Dendy, 1890b,c). *Ooperipatus insignis* was designated by Bouvier only for the Tasmanian specimens previously considered identical to the Victorian *O. insignis* (Spencer, 1895) (see Table 1).

Despite the inappropriate species designations, Bouvier considered the Tasmanian oviparous form with fourteen pairs of legs to be specifically distinct from the oviparous species with the same number of legs from Victoria. It was soon realised that *O. insignis* from Tasmania as designated by Bouvier could not retain the name assigned to it, as *O. insignis* should have been retained by precedence for the Victorian species (Cockerell, 1908). Several years later the Tasmanian species was formally designated as *O. spenceri* after its discoverer (Cockerell, 1913), and it was suggested that the oviparous species with fifteen pairs of legs and the two oviparous species with fourteen pairs of legs should not be congeneric. Hence the genus *Symperipatus* was created to accommodate *O. oviparus*, and *Ooperipatus* was retained for *O. insignis* in Victoria and *O. spenceri* in Tasmania.

Following publication of his monographs, Bouvier examined two collections of peripatus made by Dr. E. Mjoberg during two expeditions in the period 1910-1913. In the first, from Western Australia, Bouvier could identify *P. woodwardi (= gilesii)* (Bouvier, 1915). In the second, from rainforest around Cairns in northern Queensland, he identified *O. oviparus*, extending the range of that species by more than 1,000km northwards. There were, in addition, a number of anomalous specimens in which females were viviparous, but possessed an apparent ovipositor, and where males evidenced a penis-like extension of the genital region. For simplicity Bouvier included this distinctive form within *Ooperipatus*, appending the specific name *paradoxus* (Bouvier, 1914; 1915).

Recent Studies

Following the works of Bouvier and Dakin on the Western Australian fauna, little was added to the taxonomy of Australian Onychophora for fifty years. In 1938 the first photograph ever taken of a peripatus was published, incorrectly identified as *O. insignis*. The specimen, from St. Marys in north-east Tasmania, clearly displays fifteen pairs of legs and is described in the accompanying note as being of a delicate fawn colour (Barrett, 1938). We believe that this specimen may be conspecific with the 'bleached' specimen in the Macleay Museum and have recently described it, from freshly collected individuals, as *Tasmanipatus barretti n.gen. n.sp.* together with a most unusual eyeless albino form, *T. anophthalmus n.sp.* (Ruhberg *et al.*, 1991).

In 1972 Mr Robert Hardie, of the University of New England, Armidale, submitted a thesis on various aspects of the distribution, ecology, behaviour and taxonomy of Australian onychophorans (Hardie, 1972). Some aspects of this work were later published (Hardie, 1975). This study provided, for the first time, an extensive analysis of the diagnostic characters that had been used by previous authors to distinguish species. In general, the anatomical characters employed for diagnosis were shown to be unsatisfactory for a variety of reasons. These included; characteristics found in all Australian species, characteristics that displayed intraspecific variation, characteristics that were sexually dimorphic, and characteristics that altered with the stage of development. Furthermore, some characters appeared to show clinal variation with altitude and latitude. Hardie concluded that the present state of taxonomy of Australian onychophorans was unsatisfactory and, until more extensive and rigorous work was carried out, a conservative approach should be adopted. All Australian onychophorans were accordingly grouped within the one genus *Peripatoides* to include the viviparous *leuckartii* in the east and *occidentalis* and *gilesii* in the west; and the oviparous *oviparus* in eastern mainland Australia and *insignis* in southern mainland Australia and Tasmania. Along with most

other workers, Hardie ignored Dakin's (1920) synonomy of *P. gilesii* and *P. occidentalis*. Hardie considered that *O. paradoxus* (later designated *Austroperipatus paradoxus* (Baehr, 1977)) should be disregarded until further information became available. A suggestion was made that macromolecular and cytogenetic techniques could be employed to unravel the problems of morphological taxonomy displayed by the group.

A world-wide revision of the family Peripatopsidae, including the Australian fauna, completely reversed these conclusions (Ruhberg, 1985). On the basis of morphological criteria, Ruhberg divided the Australian fauna into six genera containing eight species. *Austroperipatus paradoxus* was reinstated as a valid species, *Peripatoides leuckartii* was redescribed as *Euperipatoides leuckarti* (*Peripatoides* now being reserved for New Zealand species) and its distribution extended to the northwest of Tasmania. The Western Australian species *gilesii* and *occidentalis* were included in a single genus *Occiperipatoides*. The oviparous species *Ooperipatus oviparus* was reinstated (*Symperipatus oviparus* of Cockerell, 1913). *Ooperipatus insignis* from Victoria, *O. spenceri* and *O. decoratus* from Tasmania (the last designated for specimens collected at Dip River Falls near Wawbanna, northwest Tasmania, Baehr, 1977) and *O. viridimaculatus* from New Zealand were synonymized and given a new generic designation as *Ooperipatellus insignis*. Two new species, *Mantonipatus persiculus* from South Australia and *Euperipatoides* sp. from Armidale N.S.W., were also described. This version of the taxonomic relationships of Australian onychophorans is based entirely on morphological features with emphasis on the number of legs, the number and distribution of crural papillae and associated glands in the males, and reproductive mode in the females.

In 1984 we rediscovered the form of *P. leuckartii* in the Blue Mountains which displays crural papillae on only the first pair of legs (Fletcher, 1891) and, on allozyme and morphological criteria, have described it as *Cephalofovea tomahmontis* (Ruhberg *et al.*, 1988).

Conclusions

The confusion which has arisen in the taxonomy of Australian Onychophora is attributable to several factors. First, it has been extremely difficult to find clear-cut morphological features to distinguish species and genera in such a conservative group. Second, it has generally been assumed that species would have wide distributions, for example *O. oviparus* extending from Victoria to northern Queensland (Ruhberg, 1985). While some species are widely distributed over a diversity of habitat types (Van der Lande, 1978), our allozyme analysis indicates that many species have extremely limited ranges (Tait and Briscoe, 1990) and that collections made over wide geographical areas may include, as apparently intraspecific and clinal variation, variation which is truly interspecific (cf. Hardie, 1972). Third, this confusion is accentuated by sympatry of two or more species. *Ooperipatus oviparus* and *O. insignis* coexist at Macedon in Victoria (Dendy, 1890b,c; 1891a,b,c,d). Steel (1896; 1897) recorded both *P. leuckartii* and *O. oviparus* in the Moss Vale district of New South Wales, while Bouvier (1914; 1915) described *O. oviparus* and *O. paradoxus* from the Cairns region. In our own studies we have found up to three distinct species sympatric within the same rotten log (Briscoe and Tait, in preparation).

In addition to delineating and describing the species which make up the great radiation of onychophora in Australia we are also attempting to reconstruct the phylogenetic relationships among the forms. Our colleague Dr. D. Rowell, of the Australian National University, has very recently completed polynucleotide sequencing from some of the undescribed species. His results (Rowell, 1990, pers. comm.) support the hypothesis we derived from our allozyme data, that some of the separate lineages of onycho-

phorans in Australia are extremely ancient, having diverged at a date which may well precede the break-up of Gondwana.

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Life History Characteristics of Two Sympatric Onychophoran Species from the Blue Mountains, New South Wales

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LEISHMAN, M. R. & ELDRIDGE, D. B. Life History characteristics of two sympatric onychophoran species from the Blue Mountains, New South Wales. *Proc. Linn. Soc. N.S.W.* 112 (2), 1990: 173-185.

The life history characteristics of two sympatric onychophorans, *Cephalofovea tomahmontis* and *Euperipatoides leuckartii*, were studied. The two species show differences in body size, breeding period, mechanism of spermatophore transfer, brood size, intermoult period and preferred locations of males and females within the habitat. The life history characteristics of the two species are compared with species from South Africa and South America. Variation in life history characteristics reveals a considerable diversity within the Onychophora.

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INTRODUCTION

The Onychophora are an ancient group of invertebrates that have long been of interest in phylogenetic studies. They share characteristics with both the annelid worms and the arthropods and have been claimed as a 'missing link' between these two groups (Hill, 1950; Ghiselin, 1985). Due to recent controversies regarding the origin of and the relationships between the various arthropod lineages, the Onychophora are considered either as a subdivision of the phylum Arthropoda (Ax, 1984) or as a sub-phylum of the Uniramia (Manton and Anderson, 1979).

There are fewer than 100 described species of Onychophora world-wide. The most recent revision of the taxonomy of the Onychophora recognizes eight Australian species, all belonging to the family *Peripatopsidae* (Ruhberg, 1985). However, recent electrophoretic and scanning electron microscope studies suggest that the diversity of the Australian Onychophora is far greater than previously reported (Tait and Briscoe, 1989).

Despite the evolutionary interest in the Onychophora, there is little information available on their life histories. It is known that a great variety of reproductive strategies are exhibited, ranging from oviparity through ovoviviparity to true viviparity (Anderson, 1973). Manton (1938) described fertilization, the length of embryonic development, timing of births, time to sexual maturity and longevity for four South African species of *Peripatopsis*. Lavallard and Campiglia (1975) have reported on fertilization, breeding period, brood size, parturition and time to sexual maturity for a South American species, *Peripatopsis acacioi*. There have been few studies on Australian species of Onychophora. Steel (1896) studied *Peripatoides leuckartii* in the Moss Vale area of New South Wales. He described breeding period, parturition and length of young at birth. He also speculated on time to reproductive maturity and longevity. Van der Lande (1978) described breeding season and number of embryos for the Western Australian species, *Peripatoides gilesii*. It is clear that very little is known of the life history characteristics of Onychophora in general, and of Australian species in particular.

Materials and Methods

Collection and Maintenance

Specimens of onychophorans were collected from rotting logs and leaf litter at Mt Tomah in the Blue Mountains, approximately 100km west of Sydney, N.S.W., Australia. Mt Tomah is a remnant volcanic cap of Tertiary olivine basalt (Anon, 1973) which has weathered to produce fertile soils. These soils support a diversity of vegetation communities ranging from rainforest to wet sclerophyll forest to dry sclerophyll forest, depending on altitude and aspect.

Specimens were collected from five separate locations across the mountain. At each location, $2m^2$ of leaf litter was collected and specimens were recovered in the laboratory by means of a modified Tullgren-Funnel. In addition, specimens were systematically hand-collected from all logs within an area of 4m x 50m at each location. All collections were made between mid-August and the end of October, 1986.

In the laboratory, individuals were maintained in sterile plastic containers (4cm diameter) on a substrate of moistened compressed peat. They were kept in the laboratory under ambient conditions and fed weekly on live termites or adult *Drosophila melanogaster.*

Species Identification, Sexing and Measurement

The specimens collected consisted of two sympatric species. One of these is morphologically consistent with the description of *Euperipatoides leuckartii* (Ruhberg, 1985). It has a characteristic black/blue base colour with varying numbers of brown papillae on the dorsal surface, and a pale uniform grey ventral surface. The second species has only recently been described as *Cephalofovea tomahmontis* (Ruhberg *et al.*, 1988). This species has a characteristic brown base colour with a variety of patterns of pigmentation on the dorsal surface, depending on the presence of orange, brown, green and grey papillae. The ventral surface is a uniform pale brown colour. The most characteristic feature is a cephalic pit on the dorsal surface of the head between the antennae. This cephalic pit is believed to be involved in the transfer of spermatophores from males to females, although the mechanism remains undetermined (Ruhberg *et al.*, 1988; Tait and Briscoe, 1989).

The sex of each species can be determined by external features. In *C. tomahmontis*, the cephalic pit of the females is a shallow discrete hole, while in the males the cavity is larger and extends anteriorly. Males can also be identified by the presence of a crural papilla on each of the first pair of legs; crural papillae occur at the base of walking legs and form the opening to the crural glands. *E. leuckartii* lack the sexual dimorphism on the head, however males have crural papillae on all legs except the first pair. In addition the genital opening of the female is larger and elevated on papillae, while that of the male is flattened and shorter. Subsequent dissection of specimens showed that these characteristics were reliable sex-determining features.

Body length of each individual collected was measured to the nearest millimetre as the fully extended walking length excluding antennae.

Examination of Embryos

Sixty-seven *C. tomahmontis* females and 19 *E. leuckartii* females of varying sizes were dissected in August-October and the number of developing embryos counted. The stages of development of the embryos were classified into three groups: no leg or antennae development; legs developed, head bilobed, eyes not pigmented; legs developed, head angular, eyes pigmented.

Laboratory Culture Observations

A series of observations on birth, moulting and feeding in laboratory culture were made. In August 1986, 20 adult females of *C. tomahmontis* and 10 adult females of *E. leuckartii* were housed individually. They were monitored several times daily so that parturition could be observed when it occurred. Dissections of several females of both species had revealed the presence of many well-developed embryos which indicated that birth was imminent.

Six adults and six juveniles of both species were marked at specific locations on their cuticle and were observed daily for a period of nine weeks. The mark was replaced after an individual moulted and the time between moultings was determined.

Nine 1-4 day old and nine 20-30 day old *E. leuckartii* were housed in four containers. Ten live *Drosophila melanogaster* were placed into each container and into two controls. Regular counts were made of surviving *Drosophila* over the following four days and evidence of dead and/or eaten *Drosophila* noted.

Results

A total of 428 *C. tomahmontis* (301 females, 119 males and 8 juveniles) and 88 *E. leuckartii* (28 females, 37 males and 23 juveniles) were collected.

Sex Ratio Within the Habitat

Males of *C. tomahmontis* comprised 63% of the total collected from the litter (n=43), compared to 25% of the total collected from logs (n=385). This separation of sexes between logs and litter was statistically highly significant (X^2 =12.61, df=1, $p<0.0005$). No specimens of *E. leuckartii* were found in the litter, however the proportion of males and females within logs (56% and 44% respectively, n=64) did not differ significantly from 1:1 (X^2 =0.58, df=1, $p>0.75$). Thus the sex ratio within logs was significantly different between the two species (X^2 =27.07, df=1, $p<0.0005$).

Size Distribution of the Two Species

E. leuckartii are significantly larger than *C. tomahmontis* (mean body length 23.8mm and 21.6mm respectively, t-test: T=2.43, df=70, P=0.018). The maximum recorded sizes of *C. tomahmontis* and *E. leuckartii* were 33mm and 43mm respectively (Fig.1). In both species males are significantly smaller than females (*C. tomahmontis* mean body length 17.1mm and 23.1mm respectively, t-test: T=16.94, df=318, $P<0.001$; *E. leuckartii* mean body length 21.1mm and 27.2mm respectively, t-test: T=3.39, df=31, P=0.002). For *C. tomahmontis* the maximum recorded size was 22mm for a male, compared to 33mm for a female. For *E. leuckartii* the maximum recorded size for a male was 27mm, compared to 43mm for a female (Fig. 2 and Fig. 3).

Examination of Embryos

The minimum size for a female *C. tomahmontis* containing developing embryos was 18mm (Fig. 4**a**), while almost all females greater than 18mm contained developing embryos. For *E. leuckartii* all females greater than 32mm contained developing embryos while no females smaller than this size contained embryos (Fig. 4**b**). *E. leuckartii* females contained embryos in an advanced stage of development (*ie* legs and antennae present, eye pigmentation developed) from August onwards. Females in culture also gave birth from August onwards although very few juveniles (*ie* less than 12mm) were found in the field in August and September. However in October, 39% of specimens collected were juveniles (n=*78*). In contrast, *C. tomahmontis* females did not contain well-developed embryos until September-October and no young were born in culture until October.

However the occasional juvenile was collected in the field from August to October, although the percentage of juveniles collected was never more than 5% of the total each month (n = 90 for August, n = 149 for September, n = 168 for October).

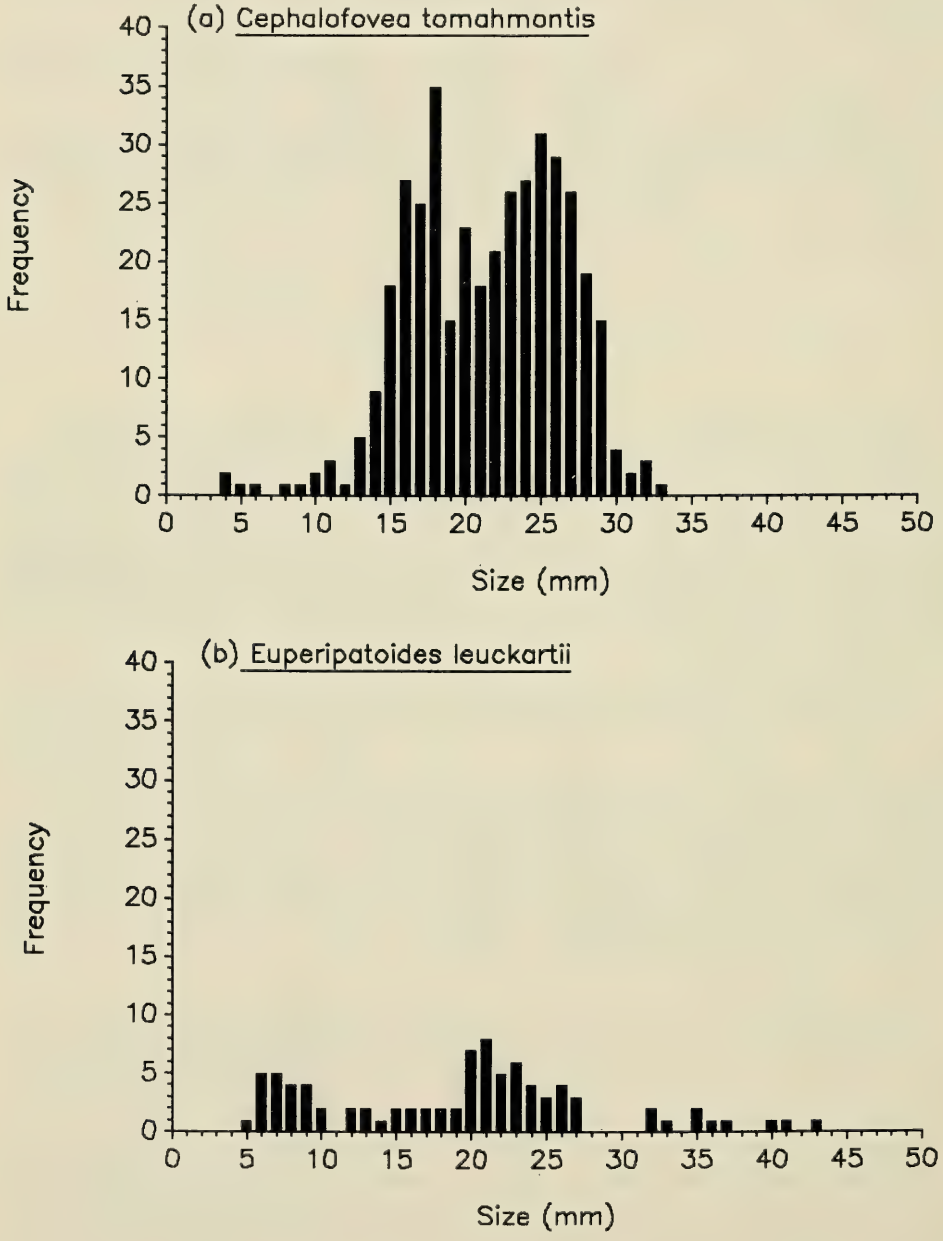

Fig. 1. Comparison of the size distribution of all specimens collected of (**a**) *C. tomahmontis* and (**b**) *E. leuckartii*.

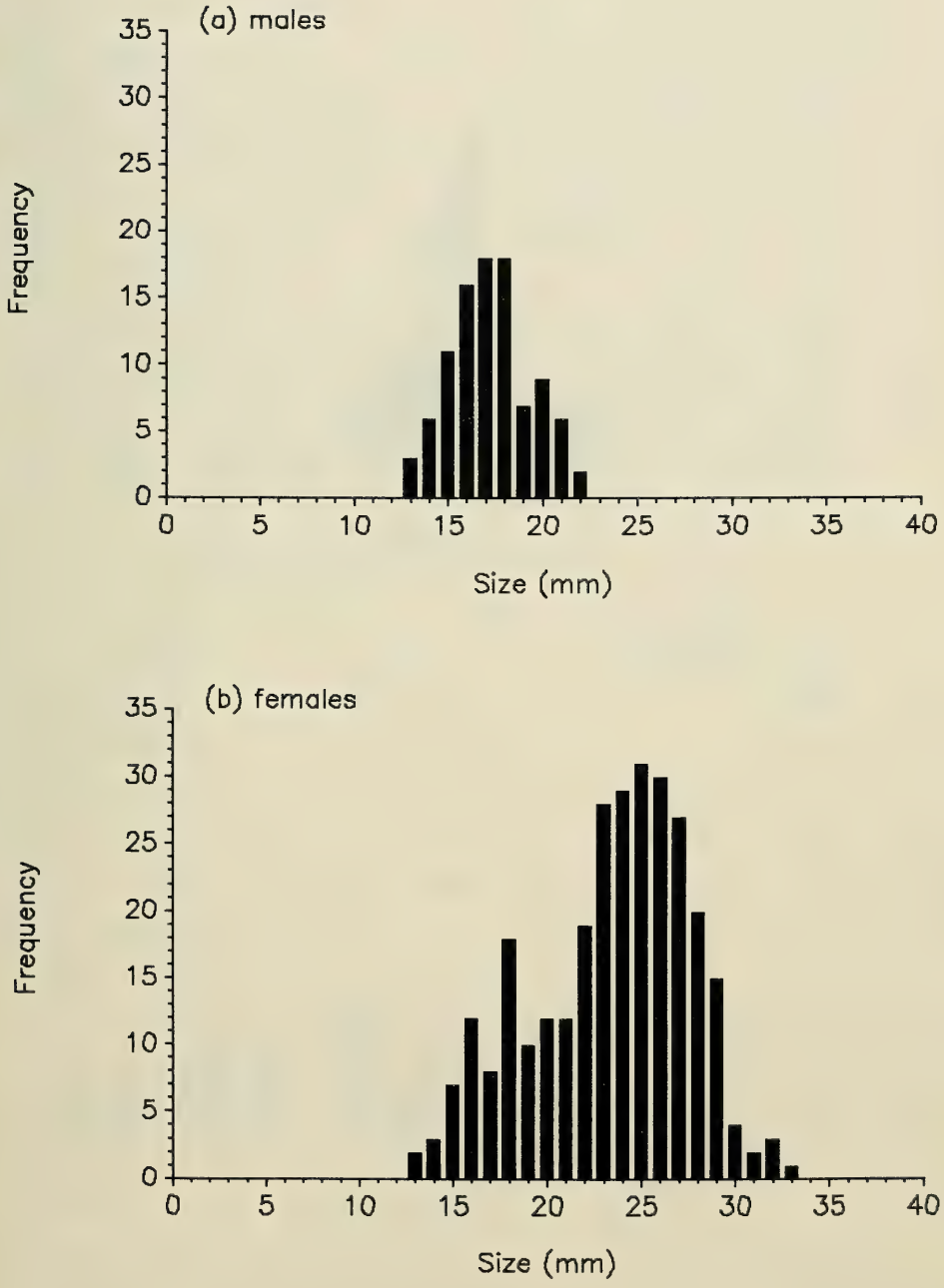

Fig. 2. Comparison of the size distribution of (**a**) males and (**b**) females of adult *C. tomahmontis*.

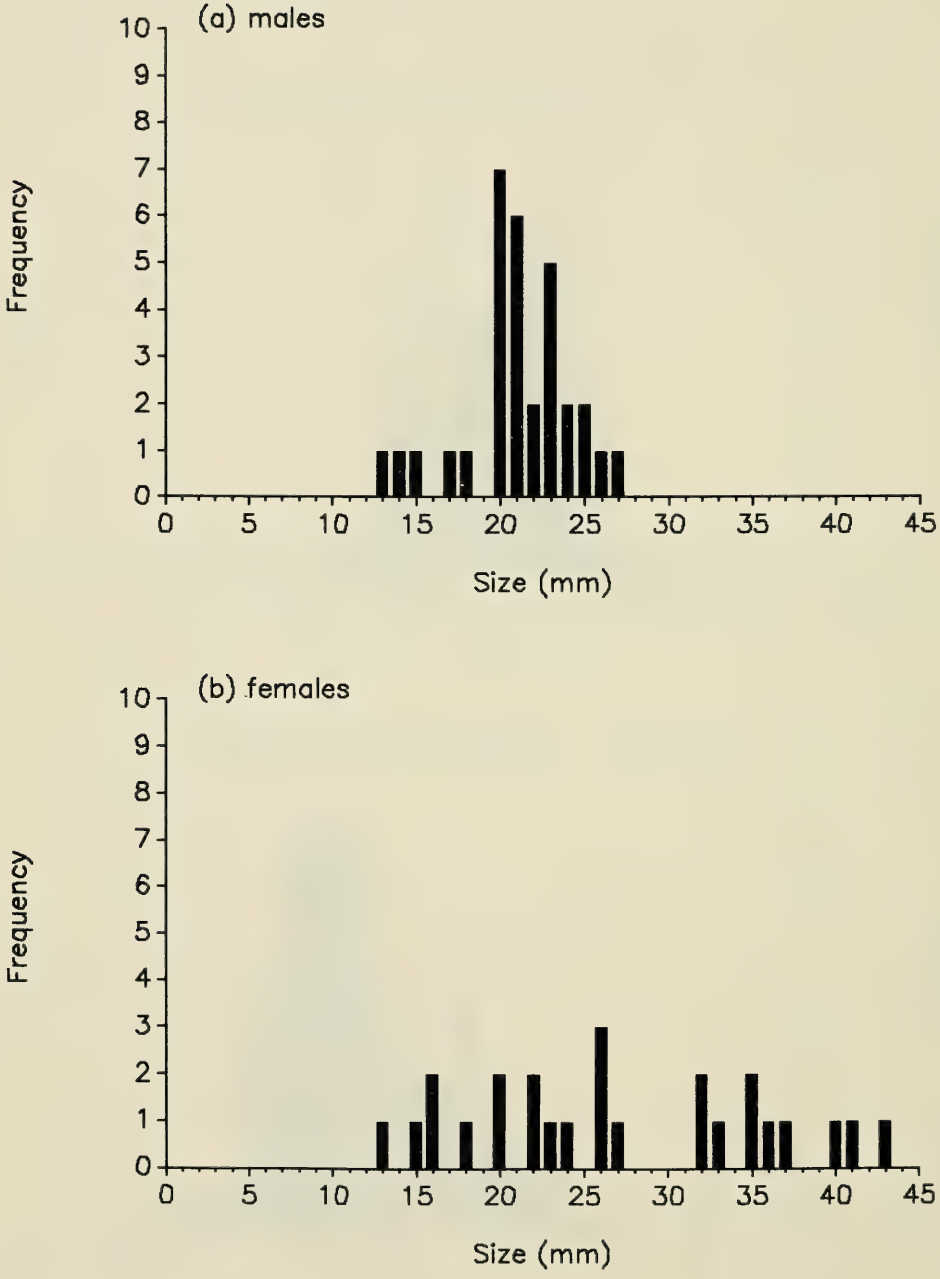

Fig. 3. Comparison of the size distribution of (**a**) males and (**b**) females of adult *E. leuckartii*.

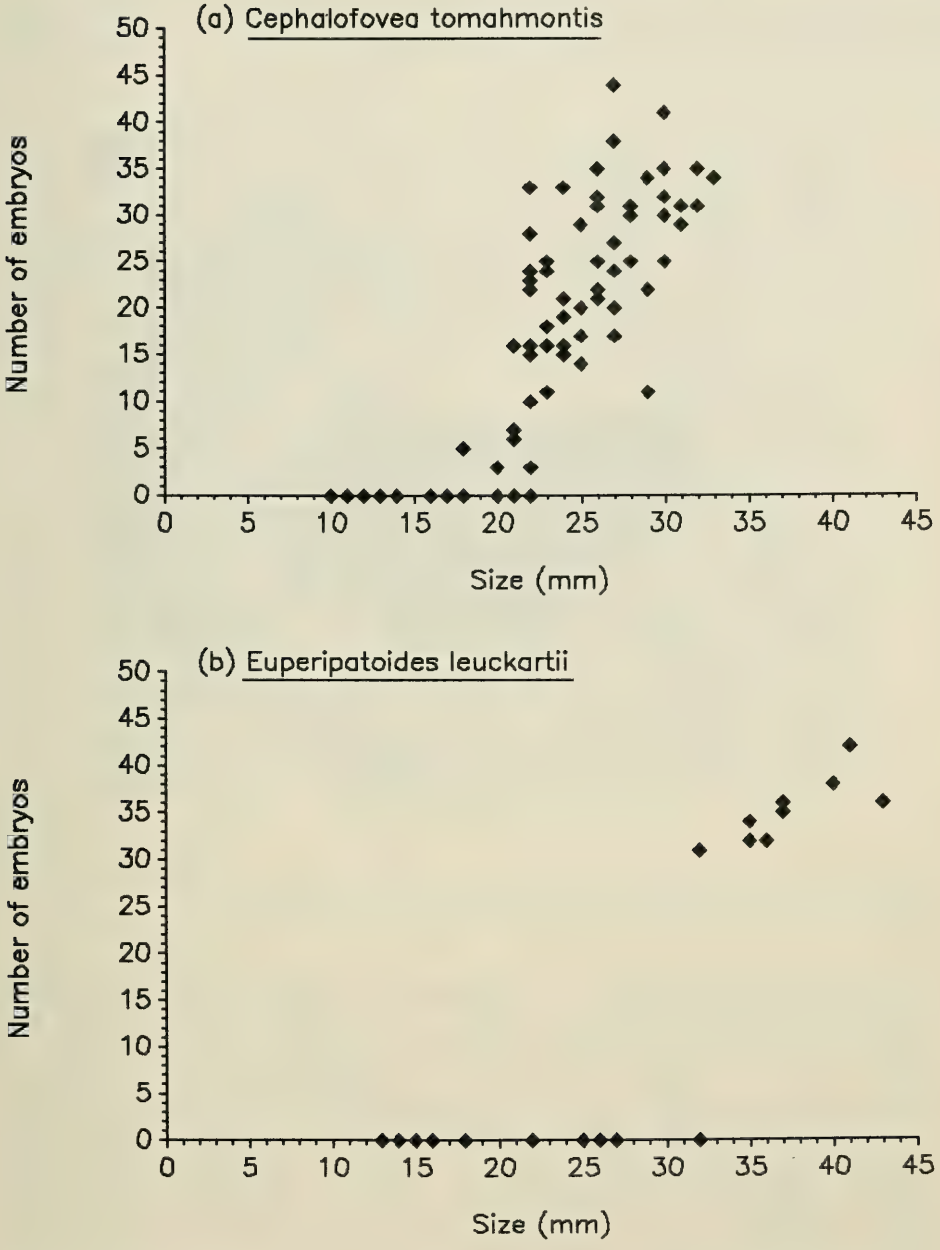

Fig. 4. Number of developing embryos within the uterus of females of varying sizes of (**a**) *C. tomahmontis* and (**b**) *E. leuckartii*.

Reproductive Status of Males

Male *C. tomahmontis* were found carrying spermatophores in their cephalic pits (see Fig. 5) between 16th September and 10th October 1986. Neither the method of deposition of the spermatophore into the cephalic pit nor the mechanism of transfer to the

female has been observed. However, several males were observed to completely evert their cephalic pit, thus presenting the spermatophore externally. The mechanism and timing of insemination in *E. leuckartii* remains unknown.

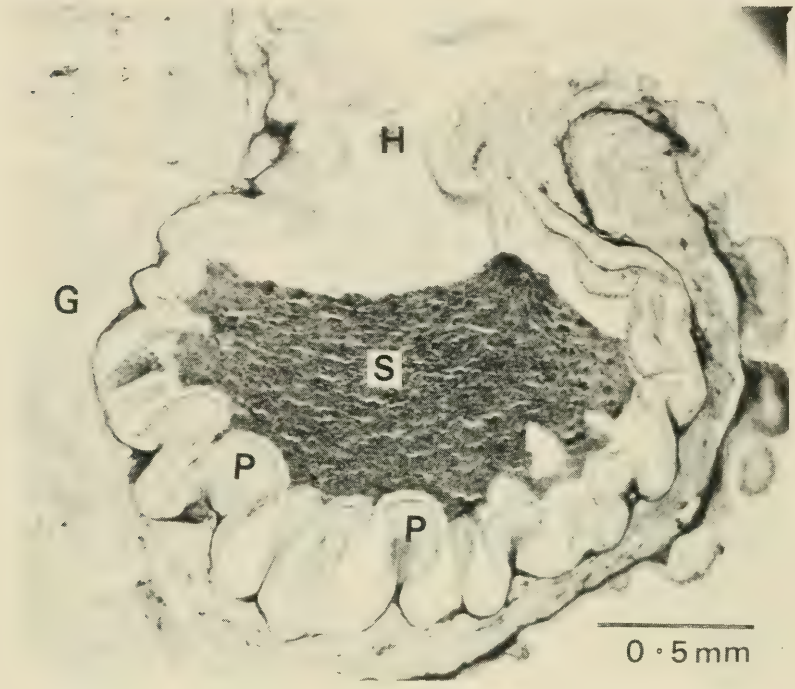

Fig. 5. Light micrograph of longitudinal section through the head of adult male *C. tomahmontis*: S, spermatophore; H, entrance to cephalic pit; P, papillae lining cephalic pit; G, cerebral ganglion.

Parturition

Both species were found to be ovoviviparous. Birth was observed for two female *C. tomahmontis* and one female *E. leuckartii*. In each case, the young were born posterior first, lying on their backs with their heads brought forward and resting on their mid-ventral surface. The young emerged still enclosed in the egg membrane which was quickly broken allowing the newborn to walk free. The length of newborn *C. tomahmontis* was 5-6mm while newborn *E. leuckartii* were 7-8mm. *E. leuckartii* were born completely white except for dark eye pigmentation, and began to develop body pigment within 10 days. Adult colouration was completed within 75 days. *C. tomahmontis* young were born a very pale brown and began to develop pigment within five days. By 22 days, the young were dark brown but lacked complete differentiation of the adult pattern. At this stage they all died due to a fungal infection.

Figure 6 shows that in both species the birth of young was spread over a period of several weeks and that frequently, several young were produced on a single day. The average number of young produced was 17.7 ± 6 ($n=15$) for *C. tomahmontis* and 26.0 ± 5 ($n=3$) for *E. leuckartii*. On the 5th November 1986, six of the *C. tomahmontis* females for which parturition had been observed were dissected. They showed no embryos remaining in the reproductive tract.

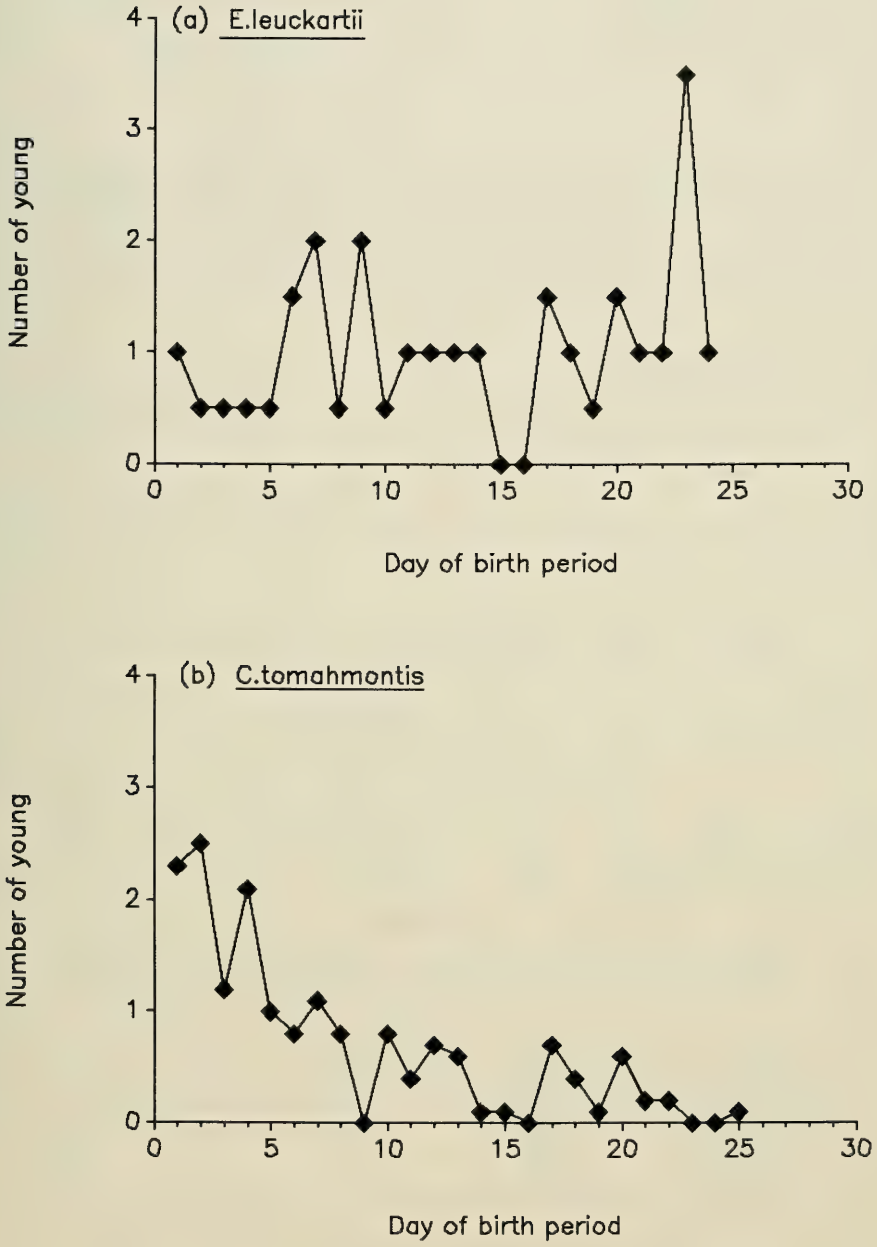

Fig. 6. Average number of young produced per day of birth period for (**a**) *E. leuckartii* and (**b**) *C. tomahmontis*.

A group of *C. tomahmontis* females collected from a single log population showed a remarkable synchronization of parturition. After spending at least 2 months housed in

separate containers in the laboratory, these females all commenced giving birth between 3rd and 5th October. On the 15th November a second group of *C. tomahmontis* females collected from a different log in August, commenced parturition. The remaining females from other logs and localities had not given birth by the end of November although dissection revealed that each contained well-developed embryos all at a similar stage of development.

Moulting

Table 2 shows that individuals of both species moulted regularly and predictably. There was a significant interspecific difference in the length of the intermoult period for both adults (t-test: T=2.2, df=29, P=0.04) and juveniles (t-test: T=2.2, df=36, P=0.05). Within each species there was no significant difference in the length of the intermoult period between adults and juveniles (*C. tomahmontis*: t-test: T=0.8, df=29, P=0.5, *E. leuckartii*: t-test: T=1.8, df=36, P=0.1).

Feeding Behaviour of Juveniles

Newly-born juveniles of both species were able to kill and eat the *Drosophila* independently of their parent (Table 1). Juveniles maintained in containers with their parents were observed to cluster around or beneath adults for the first few weeks. Similarly, they associated themselves with lumps of peat or bark and so appear to use the adults simply for physical protection. They are quite capable of surviving independently of any adult.

TABLE 1

Shows the average number of Drosophila *surviving in containers with juvenile* E. leuckartii, *as a function of time since deposited*

	TIME (hours)								
Age	**0**	**6**	**12**	**24**	**36**	**48**	**72**	**96**	**120**
1-4 day old	10.0	7.0	7.0	6.0	5.5	2.5	1.5	0.5	0.0
20-30 day old	10.0	4.0	3.0	1.0	1.0	0.0	0.0	0.0	0.0
control	10.0	10.0	10.0	10.0	10.0	10.0	5.0	3.5	0.0

TABLE 2

Shows the mean intermoult period for adults and juveniles of E. leuckartii *and* C. tomahmontis. *SD = standard deviation, N = total number of intermoult periods recorded for six individuals in each category*

Species	**Age**	**Mean**	**SD**	**N**
E. leuckartii	adult	11.5	1.9	13
E. leuckartii	juvenile	10.5	1.0	25
C. tomahmontis	adult	13.3	2.9	18
C. tomahmontis	juvenile	12.5	3.0	13

DISCUSSION

Comparison of the life history characteristics of the two sympatric species of Onychophora from Mt Tomah, N.S.W. has revealed significant differences in location of each sex within the habitat, and in body size, breeding time, size of juveniles, brood size, intermoult period and method of spermatophore transfer.

Sex Ratio and Distribution

In many previous studies of onychophoran populations, a sex ratio biased toward females has been reported. For example, Lavallard and Campiglia (1973) cite seven papers in which significantly more females than males were collected, compared to three in which more males than females were collected. In all of these studies, specimens were only sampled from one location *ie* from within and under logs.

This is the first study where specimens have been collected from different parts of the habitat including both logs and litter. Male and female *E. leuckartii* were found in equal proportions within logs. In contrast, male *C. tomahmontis* were found predominantly in the litter while females were found predominantly in logs. This illustrates the importance of sampling all of the habitat if sex ratios are calculated, and may explain the high number of female-biased sex ratios reported in the literature where specimens have been collected only from around logs. It is possible that litter does not provide sufficient protection for larger specimens of Onychophora as only *C. tomahmontis* were found in litter samples and these were predominantly male. *E. leuckartii* is significantly larger than *C. tomahmontis* and in both species, females are significantly larger than males. This sexual dimorphism is common in onychophoran species (Steel, 1896; Van der Lande, 1978; and Ghiselin, 1985).

Reproductive Status, Embryos and Parturition

Evidence from body length measurements and dissections of both species show that males smaller than any mature females had active testes and (for *C. tomahmontis*) spermatophores. Ruhberg *et al* (1988) suggest that male *C. tomahmontis* may develop sexual maturity within six months. In fact, male onychophorans are thought to be sexually precocious with some species fertile at birth (Ghiselin, 1985). Presumably for male onychophorans, early sexual development increases the number of mating opportunities while a larger size for females enables a larger brood size (see below). Steel (1896) suggested that *E. leuckartii* females first produced young at 3 years of age and lived for a further 3-4 years. Manton (1938) found that *Peripatopsis* from South Africa achieved maximum size after 3-4 years and had a total lifespan of 6-7 years.

Breeding seasons for species of *Peripatopsis* have been reported ranging from a few weeks to several months and even throughout the year (Manton, 1938; Newlands and Ruhberg, 1978). A few (less than 5% collected) juvenile *C. tomahmontis* were found in the field between August and November. In culture, *C. tomahmontis* were born from October onwards. Ruhberg *et al* (1988) found that *C. tomahmontis* females collected from Mt Tomah in February gave birth in culture from February to March. In contrast, *E. leuckartii* juveniles were found in significant numbers (39% of total collected) in the field in October. Unfortunately numbers collected in August and September ($n=3$ and $n=4$ respectively) were too low to discern demographic patterns. However, juveniles were produced in culture from August. Steel (1896) found juveniles in the field between November and March. This suggests that both species produce young during the summer months, but that *E. leuckartii* begins producing young at least 2 months before *C. tomahmontis*.

A striking aspect of the breeding pattern of *C. tomahmontis* is the apparent synchronization of births shown by females collected from the same log population, even after two months in culture in separate containers. In addition, females from the same log tend to have embryos at the same stage of development while females from another log in a separate location contain embryos at a different stage of development. This may be due to localization-effects of the population across the mountain. Electrophoretic analysis of populations of *C. tomahmontis* from three sites at Mt Tomah (Leishman, 1986) has

demonstrated significant heterogeneity in gene frequency among sites, which suggests localized substructuring of the population.

There is a large variation in brood size among onychophoran species. The two species studied differ in average number of young produced. *C. tomahmontis* produces significantly fewer offspring per brood (17.6 ± 6) than *E. leuckartii* (26.0 ± 5). Average size of newborn is larger for *E. leuckartii* (7-8mm) than for *C. tomahmontis* (5-6mm). This may be related to adult body size differences. Hardie (1975) reported that species from northern Australia, which are relatively large, produce up to 76 young, compared to 15 or so young produced by the smaller southern species. Van der Lande (1978) reported up to 15 ova within female *P. gilesii*, Holliday (1944) reported only 6-8 young per female for the South African species *P. moseleyi* and Lavallard and Campiglia (1975) reported that the annual brood of *P. acacioi* is 1-8, and frequently 2-4.

Moulting

The intermoult periods for *C. tomahmontis* and *E. leuckartii* were similar to intermoult periods observed in the South African onychophorans: *C. tomahmontis* 13.3 days, *E. leuckartii* 11.5 days, and *Peripatopsis* 14 days (Manton, 1938). However Lavallard (1977) reported a longer intermoult period of 21 days for the South American species *Peripatus acacioi*.

Reproductive Diversity

So far, we have demonstrated significant life history differences between the two sympatric onychophoran species which occur at Mt Tomah. Information from South African and South American species of *Peripatopsidae* has further illustrated the diversity of reproductive traits within the onychophorans. The method of spermatophore transfer is another good example of this diversity. Lavallard and Campiglia (1975) report for *P. acacioi* that fertilization takes place once only by way of the vagina when females are 5-9 months old. In contrast Manton (1938) and Holliday (1944) found for the South African species *P. moseleyi* and *P. sedgwicki* that spermatophores were deposited at random on the exterior of females and entered the haemolymph through an ulcer which develops in the body wall. Other species have been reported to possess spermatophores with a hollow spine which is stabbed into the female allowing the sperms to pass down the spine into her body (Paling, 1969). In *C. tomahmontis* the spermatophore is located in the cephalic pit on the male's head. This cephalic pit can be everted to present the spermatophore externally and presumably to transfer the spermatophore to the female. No such mechanism exists for *E. leuckartii* or has been reported for any other species. Further studies should reveal much useful and interesting information on this ancient but little known group of invertebrates.

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Comparative Plant Ecology and the Quest for Understanding of Australian Plants

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SYNOPSIS

Understanding the Australian flora involves, firstly, knowing what plants make it up and where they occur, secondly, knowing their origins in geographical and evolutionary terms, and, thirdly, knowing how they inhabit their respective habitats and interact with other components of their environment. The first two sets of knowledge are being addressed on an institutional basis in herbaria across Australia. The third has yet to be tackled in any organized institutional way. It is suggested that this be started, and that attributes of plants be described and compared over all stages of their life cycles to seek relationships between syndromes of plant attributes and ranges of habitats occupied by them.

INTRODUCTION

The discovery by Europeans of eastern Australia and some of its flora occurred in the lifetime of Linnaeus. At a meeting of the Linnean Society of New South Wales, it is thus appropriate to examine briefly directions scientific understanding of Australian plants has taken and might take in future.

The basic question of what plants are in the flora is still being solved. Describing and naming the vascular plants have progressed considerably, but knowledge of non-vascular plants in the flora is scant (see, for instance, Briggs and Leigh, 1988). Much basic taxonomic work remains to be done, simply describing and naming species in our flora.

Questions of origin in Australian plants are being put and being at least partially answered in a geographical sense (see, for instance, Barlow, 1981 and White, 1986) and in the relatedness of plants within groups through cladistic, palaeontological and genomic analyses. Without doubt, such studies will continue to be an adjunct and, to some extent, a spur to basic taxonomic work.

In the course of basic taxonomic work, other kinds of questions are examined. These include distributional questions, principally in a geographical sense but in ecological terms also. Together with work on distributions of individual species, types of vegetation are identified and mapped. Notable pioneering works of this latter sort are those of Beadle (1948) in his mapping and description of the vegetation of western New South Wales and of Costin (1954) in the Monaro.

From patterns of distribution follow questions of why particular species of plants occur where and when they do. It is these questions and closely related ones about their abundance that are ecological. Ways of seeking answers to them are almost as many as there are ecologists, and opinions differ sharply on valid approaches to ecological analysis (see, for instance, Harper, 1982 and Grime, 1984). As Grime (1979) points out, the approaches can be put into three sorts: the correlative, direct and comparative.

The correlative approach seeks to establish correlations between distributions of species and types of vegetation and environmental variation, and uses the correlations to formulate hypotheses about critical factors controlling populations of plants and variation in vegetation.

In the direct approach, essential events in survival and reproduction of individual plants in wild populations are examined and used to find out how the distribution and abundance of plants are controlled in particular populations. It is mostly short-lived herbs that have been studied in this way — see, for example, work reviewed in Harper, 1977. However, some of our local species of woody plants, regeneration of whose individuals or clones is triggered by fire, have also been been studied and some factors controlling their distribution and abundance successfully identified, for example, in *Angophora hispida* (Auld, 1986), *Acacia suaveolens* (Auld, 1987), *Banksia ericifolia* (Bradstock and O'Connell, 1988; Zammit and Westoby, 1988), *B. oblongifolia* (Zammit, 1988; Zammit and Westoby, 1988), *B. serrata* and *Isopogon anemonifolius* (Bradstock and Myerscough, 1988), and *Petrophile pulchella* (Bradstock and O'Connell, 1988).

The comparative approach examines attributes of plants through their life cycles and from them seeks to understand how species of plants occupy specific ranges of habitat. This was attempted in a general way on a world-wide basis by Schimper (1903), but the understanding achieved was necessarily very preliminary and was not based on detailed studies of individual species in a flora. Recently, the Unit of Comparative Plant Ecology in Sheffield, formed on the initiative of Clapham (1956), celebrated 25 years of its existence (Rorison *et al.*, 1987) and published a major compilation and synthesis of its work (Grime *et al.*, 1988). This presents detailed accounts of attributes of some 281 common species of British vascular plants and some details of some 221 other species. It is pertinent to ask whether significant advances in our understanding of Australian plants would be made by such long-term detailed work done on a similar institutional basis to that suggested by Clapham (1956). To do this, it is firstly necessary to outline the essential elements of comparative plant ecology, and then to examine how it has been used in Australia.

The Elements of Comparative Plant Ecology

As in any ecological analysis, the essential elements are environments and organisms. Comparative ecology seeks to handle the ranges of variation in both, and to examine the extent to which particular ranges of attributes of species fit into particular environments.

Environmental variation is mostly handled by some form of classification. Ideally, only physical characteristics of the environment, measured independently of the vegetation, should be used, to avoid circularity in interpreting occurrences of plants in habitats.

With the attributes of plants, all aspects of the life cycle, growth, reproduction, dispersal, germination and establishment, have to be covered. In examining their variation, it is convenient to divide the life cycle into two complementary phases, the regenerative and established phases. This division is common to Grime's system (Grime, 1979; Grime *et al.*, 1988) and to that of Noble and Slatyer (1980). In each system, the regenerative phase covers not only dispersal, germination and establishment through seed or spores, but vegetative re-establishment after loss of leaf canopy and clonal reproduction. The two phases are clearly differentiated in the plant's relationship to resources and mobility. Essentially, on land in the established phase the plant is attached to one place and, if successful, is gathering energy and other resources, increasing its size and

reproductive potential, while in the regenerative phase it is not gathering resources and may be in a form that is dispersed.

Regenerative and established phases of the life cycle are variously related in plants, and this variation is obviously pertinent in variation in occupation of habitats by plants. This can be illustrated by examining four broad types of relationships between seed banks, the dormant, viable seed present, and established plants:

- seed bank ephemeral and growing plants continuously present. This sort of relationship, apparent in many rainforest species, clearly implies an environment in which whole populations of growing plants are not periodically destroyed by disturbance, such as drought, fire, cyclone or clearing.
- seed bank permanent and growing plants ephemeral. This sort of relationship, characteristic in plants of periodically disturbed habitats, is apparent in a whole suite of species in the flora of central Australia.
- seed bank and growing plants both continuously present. This type of relationship occurs in many herbaceous species of temperate grasslands.
- neither seed bank nor growing plants continuously present. This occurs in some species of plants which occur where water is available on a strictly seasonal basis, e.g. *Sorghum intrans* in northern Australia (Andrew and Mott, 1983), and in some species in vegetation that is burnt from time to time, for example *Banksia ericifolia* in vegetation on sandstones in the Sydney region (Siddiqi *et al.*, 1976; Bradstock and Myerscough, 1981; and Zammit and Westoby, 1987).

To provide some basis for comparison for what has been and might be attempted in Australia in comparative plant ecology, it is useful to outline what the Unit of Comparative Plant Ecology in Sheffield has done. In the full summary of the work (Grime *et al.*, 1988) attributes of 281 species of British vascular plants are compared. Central to this comparison is a three-cornered ordering of the species on their attributes taken from all stages of the life cycle. The three extreme syndromes of attributes, strategies in the terminology of Grime (1974), against which each species is ordered, are, in terms of the attributes most useful in identifying them (see Table 3.3, pp. 23, 24, of Grime *et al.*, 1988):

- competitive: shoots with extensive lateral spread and rapidly-ascending dense canopy of leaves in a monolayer with well-defined peaks of leaf production coincident with periods of maximum potential productivity; photosynthetic products and mineral nutrients rapidly incorporated into vegetative structure but a proportion stored for growth in next growing season; potentially high mean relative growth rates.
- stress-tolerant: long-lived plants with evergreen, often small or leathery leaves and long-lived roots and intermittent flowering and often persistent juveniles; low palatability to unspecialized herbivores; potential mean relative rates always low.
- ruderal: very short-lived plants of small stature and limited lateral spread, flowering early in their life-history and devoting a high proportion of annual production to seeds; potentially high mean relative growth rates.

The three extremes approximate, in the system of Southwood and Greenslade (Southwood, 1988), to K-, adversity- and r-selected species respectively. Most species fall somewhere between the three extremes in their syndromes of attributes. In terms of habitats occupied, plants with ruderal syndromes occupy those disturbed frequently, and plants with competitive syndromes those not disturbed and in which resources are freely available, while plants with stress-tolerating syndromes occupy habitats which are not disturbed but are short of one or more resources for plant growth. According to Grime (1977), should frequent disturbance cease in a habitat, the ruderal plants initially

present are replaced firstly by those with competitive syndromes and finally, as resources for plant growth become short, by plants with stress-tolerating syndromes.

Use of Comparative Plant Ecology in Australia

In Australia, Rogers (1988) used the system of Grime (1979), with its triangular ordination of syndromes of plant attributes, in a study of lichens on a palm trunk in Brisbane. He estimated relative growth rates and other attributes of the species of lichens studied and used them to draw axes in triangular ordinations and place each species at a point in each of the ordinations he drew up and examined. He could age the surfaces on the trunk and show that, in time, species with ruderal syndromes according to his ordinations were replaced by those with competitive syndromes.

Generally the system of Grime and his colleagues has been used little other than by him and his colleagues in Sheffield. Use of the comparative approach in Australia and elsewhere has been in other ways. It has largely been directed to one of three ends: understanding temporal relationships between species following disturbance in a habitat, especially fires; understanding habitat differentiation between species of plants and types of vegetation; and understanding ecological differences and similarities between species or higher taxonomic groups of plants.

Temporal Relations Between Species

The system of Noble and Slatyer (1977; 1980), using broad categories of plants in both regenerative and established phases of their life cycles, is largely directed to understanding temporal changes in vegetation following disturbance, especially fire. Their categories in modes of regeneration of plants are closely related to those of Gill (1981) — see Noble (1981). Their system has mostly been used to model changes in temperate forests under various regimes of disturbance. The models proposed require testing, and details of the regenerative and established phases in some of the plants on which the models are based also require confirming.

Habitat Differentiation Between Species

Appreciation of differences between habitats and of general differences of plant attributes between broad classes of habitat has long been characteristic of plant ecology in Australia. In the moist climate of eastern Australia, the difference between rainforest and sclerophyllous vegetation and its relationship to habitat have been explored in the work of Beadle (1954; 1962; 1966; 1968). Within rainforest, variation in leaf characteristics with habitat was clearly shown in Webb's work (1959). As Specht (1970) points out, Diels (1906) drew attention to the variation of hardness of leaves with habitat, leading to the use of the term 'sclerophyll' in the description of certain types of vegetation in Australia.

Leaves are probably one of several plant attributes that vary with habitat. For instance, it is apparent that as soil fertility decreases the proportions of species with serotinous fruits and of those with seeds bearing elaiosomes increase (Milewski and Bond, 1982; Westoby *et al.*, 1982), while the proportion of species with large fleshy fruits decreases, as the vegetation becomes more sclerophyllous and heathy (see, for instance, Milewski and Bond, 1982). It is clear that systematic study of attributes of plants in both their regenerative and established phases in any climatic regime would lead to greater understanding of how various suites of species occupy different parts of gradients of soil fertility.

Ecological Differentiation Between Species or Groups of Species

Comparisons between species over all stages of their life cycles have been made to

understand both their occupancy of different habitats and their co-existence in certain other habitats — see, for instance, Williams' (1979) comparison of *Atriplex vesicaria* and *Maireana pyramidata*. Wider comparison has been made by Noble (1989) between two eucalypt subgenera, *Monocalyptus* and *Symphyomyrtus*. Although it is necessarily based on sketchy and scattered data, it shows that general differences in attributes between the subgenera may explain, among other aspects of ecological differentiation, the frequent co-existence of species of the two subgenera in various types of vegetation. It is clear that comparison of pairs of species or of larger groups of species is one way in which some understanding of both differentiation between species in occupancy of habitat and mechanisms of co-existence in the same habitat may be achieved.

Prospects for Use of Comparative Plant Ecology in Australia

Understanding of Australian plants can be greatly increased by systematic work in comparative plant ecology, and the sorts of studies of habitats and attributes of plants required for this can be suggested.

Habitats

Climatic variation is a major consideration in Australian habitats. Major differences of temporal and spatial patterns occur between vegetation of areas where rainfall is usually adequate for plant growth in many months of most years and that of semi-arid and arid areas where moisture is available irregularly for very variable periods. In arid and semi-arid areas, biomass and the relative contributions of particular species in it may vary over several orders of magnitude with amount and season of rainfall — see, for example, Robertson (1987). Conversely in areas where rainfall is greater and more reliable, biomass and the relative contributions of particular species to it vary much less with variation of rainfall in time.

Within climatic zones, site characteristics vary, including soil fertility — see, for instance, Nix (1981). In freely draining sites in both arid and humid areas there is variation of vegetation with fertility. For instance, in arid areas as the clay content of soils declines and they become sandier or rockier there is an increase in xeromorphic grasses of *Triodia, Plectrachne* or *Xerochloa* spp. present in the vegetation (Beadle, 1981).

Clearly, if systematic studies in comparative plant ecology were to be undertaken in an extensive way in Australia, seeking relationships between plant attributes and habitat characteristics, a treatment of habitat characteristics would be required that would be independent of the vegetation present in given sites. Such independent treatment could be achieved in terms of some physical characteristics of sites but would be less easily achieved for nutrients and other chemical characteristics in soils due to plant-soil interactions. Any classification of habitats needed almost certainly would be firstly by climatic zones and then by specific site characteristics.

Plant Attributes

Established Phase

Established plants take up energy and other resources. Their attributes are thus likely to be related to availability of resources, both at the shoot and the root.

Stance of leaves appears to be primarily related to availability of water and control of temperatures within tissues, but has secondary implications in productivity of canopies of leaves. Australia is a continent that has dried out relatively recently in geological terms, and it lacks the large succulent-stemmed plants found in some of the drier regions of both New and Old Worlds. Leaves of many longer-lived plants of Australia's arid and semi-arid areas tend to hold their flattened surfaces vertically rather than

horizontally. Such a stance facilitates the transfer of sensible heat to the atmosphere when water is unavailable for significant transpiration, and in dry conditions leaves with vertically held surfaces maintain cooler tissues than do similar leaves with horizontally held surfaces (Mooney *et al.*, 1977). In Australia, a predominantly horizontal stance of leaves only occurs in the scattered rainforest of the eastern coast. The vegetation of much of the rest has more nearly vertical displays of leaves.

Vertically held leaf surfaces are not only more streamlined to transfer of sensible heat to the atmosphere than horizontally held leaves they are potentially more efficient in the uptake of carbon dioxide when they are saturated with light and their stomata are fully open (Larcher, 1980). This is probably part of the explanation for very rapid growth in certain eucalypts, such as *Eucalyptus grandis* and *E. pilularis*, which colonize large gaps on moist, fertile sites in the coastal region of northern New South Wales. Their canopies are also multilayered in the sense of Horn (1971) and for this reason also are likely to be highly productive. Conversely, many species of rainforest tree have horizontally held leaves and may have monolayered canopies in Horn's sense, and, as such, grow more slowly than the eucalypts but are more shade-tolerant and eventually may suppress the eucalypts. Such replacement of eucalypts by rainforest species is outlined in the schemes of Noble and Slatyer (1977; 1980). In short, a vertical leaf stance that may be primarily related to control of leaf temperatures under water stress may also be an important component of the rapid growth of certain eucalypts.

Shoot and root characteristics appear to vary across gradients of soil fertility. In the infertile sand of Dark Island Heath, the data of Specht *et al.* (1958) show large proportions of root in the biomass of the plants, about 75%, compared with 20% to 25% in many forests (Rodin and Bazilevich, 1967), indicating that the organs collecting the resources in short supply are highly developed, while Beadle (1966) has argued that the xeromorphism apparent in shoots of plants on infertile soils is functionally related to their sparing use and conservation in live cells of the plants.

In short, there are already some general lines of understanding variation in attributes of established plants in relation to availability of resources. They require further testing, and one way of doing so is by detailed comparative studies of the attributes across wide ranges of species and environments.

Regenerative Phase

In the regenerative phase, general relationships also appear to exist between plant attributes and environmental characteristics, especially along gradients of resource availability.

Soil fertility affects vegetation and the way it responds to fire. Under infertile conditions, litter is not broken down as rapidly as under fertile conditions (see, for instance, Florence and Lamb, 1975), and, being low in nutrients, phosphorus in particular, such litter is more flammable when dry than that of vegetation from fertile sites. In Australia, seed banks of plants in sites of low fertility show many characteristics in their release, dormancy and germination that are closely related to the incidence and types of fires in such sites — see, for instance, Gill (1981).

The size of seeds may show relationships with variation in habitat. In Britain, Salisbury's (1942) work showed a tendency for seed weight to increase with the shadiness of the habitat in which seedlings of species normally become established, while, in California, a study by Baker (1972) found a similar tendency for seed weight to increase with dryness of habitat. In Australia, it is possible that seed weight may increase in closely related taxa across gradients of decreasing fertility. Work with *Angophora* species in the Sydney region (Mowatt, 1981; Mowatt and Myerscough, 1983) showed that *A. hispida*, a species confined to infertile sites, had the highest mean seed weight while *A.*

floribunda, a species occurring on better sites, had the least, while mean seed weight of *A. costata* was between them both in seed weight and occupancy of sites on a gradient of fertility. A recent study of *Chionochloa* species in New Zealand (Lee and Fenner, 1989) has also shown a similar converse variation of seed weight with fertility of sites occupied by the species. It is also possible that seeds of species occurring in infertile sites may contain a higher proportion of mineral nutrients by weight than those of species from more fertile sites. This was not borne out in the study of *Chionochloa* species by Lee and Fenner (1989), but work of Grundon (1972) showed that seeds of Proteaceae taken from Queensland heath had higher proportions by weight of phosphorus than seeds of other species he tested, including some cultivated species. It is clear that possible relations between site fertility and seed weight and content of mineral nutrient require examining across a range of Australian species and habitats.

Variation in seed weight in relation to availability of resources for establishing seedlings, water in species in the Californian flora (Baker, 1972), light in species in the British flora (Salisbury, 1942) and possibly soil nutrients in Australian plants, can be expected where supplies of resources to the developing seedlings have under selection outweighed constraints on seed size imposed by dispersal or predation of seeds or constraints intrinsic to the development of the fruit or seed itself. The relative importance of such contraints under past selection may be assessed after seed weights have been examined across a range of species.

In Australian rainforests, there are frequently significant numbers of persistent seedlings on the forest floor. Such banks of persistent seedlings may be characteristic of a number of rainforest species and may not occur extensively outside rainforest in Australia. The persistence of such seedlings may depend on mycorrhizal associations through which seedlings may obtain sufficient carbon to maintain slow growth under shade that may be close to the compensation point for net photosynthesis for much of the time. Preliminary work with mycorrhizal and non-mycorrhizal seedlings suggests that this may be so in *Ceratopetalum apetalum* (P. A. McGee, personal communication). The persistence of seedlings and its possible relationship with habitat should be examined across a range of species and habitats in Australia.

Questions for Investigation

Questions to be faced in a systematic ecological comparison of attributes of plants in Australia include:

- What sort of classification, or ordering, of habitats would be the most productive basis across which to compare attributes of plants? Part of an answer to this may be to organize habitats according to where they lie along gradients of soil fertility and drainage within specific climatic zones.
- Are syndromes of attributes of plants likely to be of characteristic types within particular sets of habitats? Preliminary evidence certainly suggests that this is so, both with variation in soil fertility, as indicated above, and with variation in soil drainage. Marked physiological differences appear to exist in the established phase of plants between those that occur in waterlogged habitats and those that do not.
- Can syndromes of attributes be used to predict temporal and spatial relationships between plants? The work of Noble and Slatyer (1977; 1980) indicates that temporal relations may be predicted and could be tested in some situations. Coexistence of species may also be analyzed in terms of attributes of plants and environmental variation in space and time — for instance, see Yen and Myerscough (1989a, b).

- How may syndromes of attributes of various species be profitably classified or ordered? The triangular ordination of Grime (1974) is probably not what is required initially. It is within a confined framework, a framework which carries with it a large amount of interpretation. Initially, some form of open-ended classification, perhaps based on the classes of syndromes of Noble and Slatyer (1977; 1980), would probably be much more useful.
- Are specific sorts of syndromes of plant attributes linked not only to particular ranges of habitat but associated with particular types of breeding system? This sort of question was pursued by Heslop-Harrison (1964) and Baker and Stebbins (1965).

Limits of Comparative Ecology

Comparison of syndromes of attributes of plants, though highly useful in understanding occupancy of habitats and temporal relations of plants, can not conclusively reveal significant interactions that underlie their patterns of distribution and dispersal. These can only be properly investigated by direct means of careful experimental work in the field (Harper, 1982). Ecological understanding of plants may be best achieved through a combination of the comparative and direct approaches, the first providing both the context and hypotheses for the detailed experimental work in the field of the second.

Contributions of Comparative Plant Ecology to Other Botanical Disciplines

Contributions of comparative plant ecology are relevant in at least two other areas. Firstly, it is relevant in management of plant populations. In relation to fire, Bradstock and Auld (1987) seek what they term 'indicator species', species characteristic of particular syndromes of attributes and which are either particularly slow or rapid to pass through certain stages of their life cycle, to study reaction of their plants to various aspects of burning in both humid and more arid vegetation. Recognition of such 'indicator species' is clearly an important contribution of comparative plant ecology. More generally, knowledge of syndromes of species may be vital in ecological restorative work in the next century. Such work might include making wildlife corridors to link otherwise isolated nature reserves or national parks, as suggested in a recent submission of the Society on coastal development (Linnean Society of New South Wales, 1990).

Secondly, in gathering data on attributes of plants over the whole life cycle, comparative plant ecology could provide information not only relevant to understanding ecological distributions of species but also useful in taxonomy, allowing alpha-taxonomy to progress toward omega-taxonomy in the sense of Turrill (1938).

Conclusion

Botanical understanding is progressing from the basic question of what plants are in the Australian flora to questions of origins of the plants. Beyond these questions are questions of how the plants fit into environments, questions of control of their distribution and abundance. As Clapham (1956) argued, comparative plant ecology can make a tremendous contribution in bringing answers to such questions, especially if pursued on an institutional basis, geared to the long-term goal of finding out in an organized way the attributes of the plants over both the regenerative and established phases of their life cycles.

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The Geology of the 'Glendale' Area, Near Kandos, New South Wales

ALEX G. COOK

COOK, A. G. The geology of the 'Glendale' area, near Kandos, New South Wales. *Proc. Linn. Soc. N.S.W.* 112 (4), 1990: 201-212.

In an area centred on the rural property of 'Glendale', west of Kandos, N.S.W., Early Devonian sediments and volcanics are faulted against Late Devonian strata and are unconformably overlain by basal Permian elements of the western Sydney Basin.

The Early Devonian sequence consists of the *Yellowmans Creek Beds* (oldest), *Roxburgh Formation*, *Riversdale Volcanics* and *Carwell Creek Formation* (youngest). Late Devonian strata are the older *Buckaroo Conglomerate* and younger *Bumberra Formation*.

Permian sediments in the south of the area, are the *Megalong Conglomerate* (oldest), *Berry Siltstone*, and *Illawarra Coal Measures* (youngest).

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INTRODUCTION

Mapping centred on the 'Glendale' area near Kandos, New South Wales, has delineated an extensive explosive silicic volcanic sequence within a shallow marine, predominantly clastic Early Devonian succession; shallow marine units of the Roxburgh Formation and Carwell Creek Formation are separated by up to 890m of ignimbrite, volclitharenite, ash tuff, conglomerate and sublitharenite of the Riversdale Volcanics. These Volcanics have, elsewhere in the region, traditionally been regarded as shallow marine (Pemberton, 1977; Millsteed, 1985); however, stratigraphic, sedimentologic and textural information suggest that the Volcanics are largely a mixed subaquaeous and subaerial succession.

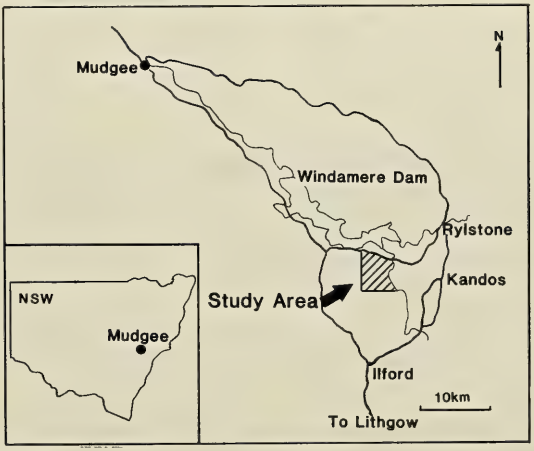

Fig. 1. Location of study area.

Previous geological investigations in the area includes the work of Sussmilch (1933) whose illustrated geological cross-sections include the 'Glendale' area and Game (1935) who interpreted the porphyries near 'Glendale' to be intrusives. More recent work in the district includes that of Pemberton (1977, 1980), Campbell (1981) , Millsteed (1985), Cook (1988) and Colquhoun (pers. comm.).

Location and Stratigraphic Framework

The 'Glendale' area is situated on the Capertee Anticlinorium (Scheibner, 1974) and contains Early Devonian strata characteristic of the Capertee High of Packham (1969). 'Glendale' lies 7km to the west of Kandos, approximately 40km SE of Mudgee and 250km NW of Sydney (Fig. 1). The sequence (Fig. 2) consists of the Yellowmans Creek Beds (Millsteed, pers. comm.), Roxburgh Formation (Pemberton, 1980), Riversdale Volcanics (Wright, 1966) and Carwell Creek Formation (Offenberg *et al.*, 1971), which is the youngest exposed Early Devonian unit. The surface geology of the 'Glendale' area is outlined in Fig. 3.

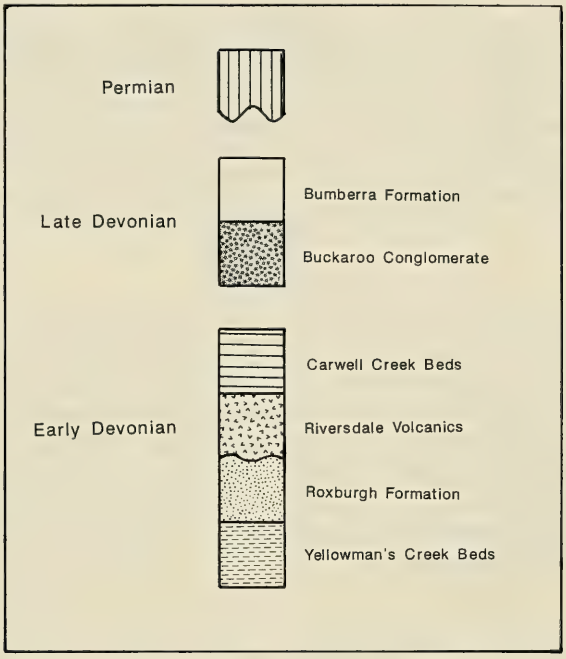

Fig. 2. Generalized stratigraphy within the study area.

The Late Devonian Buckaroo Conglomerate (Wright, 1966) and Bumberra Formation (Wright, 1966) crop-out to a subordinate extent within the study area.

The post-Devonian strata include essentially flat-lying elements of the western Sydney Basin sequence, which unconformably overlies the folded Devonian strata and consists of the Megalong Conglomerate, Berry Siltstone, and lower units of the Illawarra Coal Measures.

Stratigraphy

Yellowmans Creek Beds

The Yellowmans Creek Beds (Millsteed, pers. comm.) is the oldest unit exposed within the 'Glendale' area, cropping-out within the NE portion of the study area. The base of the unit is not seen within the study area, but a thickness of more than 340m is present. The Yellowmans Creek Beds are conformably overlain by the Roxburgh Formation.

The Beds are composed of finely-laminated shales and fine sandstones, green to brown in colour and commonly cleaved. The unit becomes slightly coarser, lighter in colour and more quartzose towards the top of the Beds. Characteristic mineralogy is

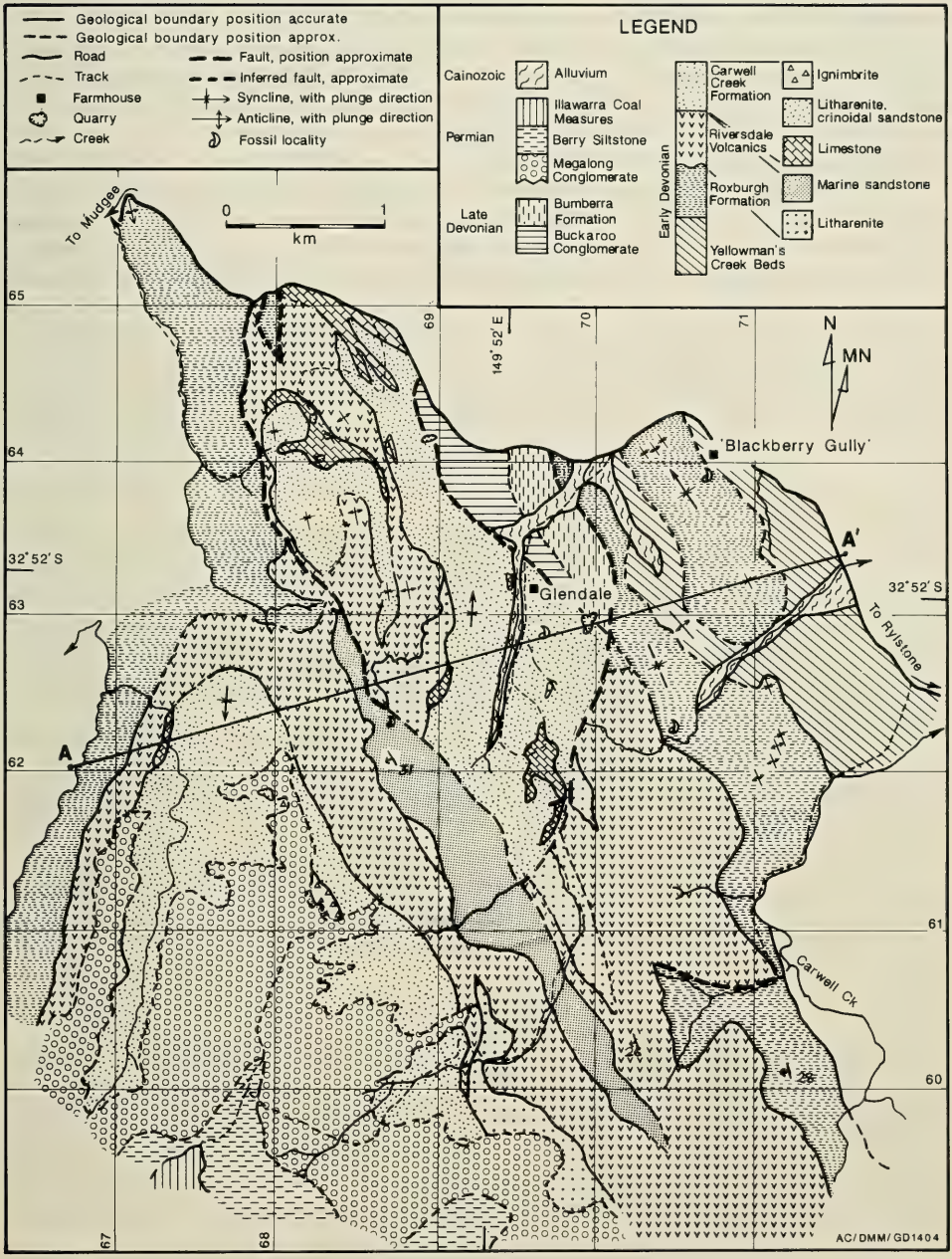

Fig. 3. Surface geology of the 'Glendale' area, showing location of cross-section A-A[1] (Fig. 5).

abundant fine-grained quartz, muscovite, chlorite and minor hematite with scattered larger quartz grains. Dark stringers of organic matter are common.

The only fauna found within this unit in the study area were a few crinoid ossicles and a fragment of an ?isorthid brachiopod. Millsteed (1985) reports a Lochkovian fauna from limestone pods within these Beds to the NW. The marine fossils, fine-grained lithology, starved asymmetrical ripple marks and parallel-laminated bedding highlight quiet marine conditions.

Roxburgh Formation

The Roxburgh Formation (Pemberton, 1980) crops-out extensively near both the eastern and the western margins of the study area. To the west the Formation, of which the base is not seen, is represented by more than 400m of strata, and this is only part of the 850 + m thick sequence originally described by Pemberton (1980); to the east the total stratigraphic thickness is 125m. The Roxburgh Formation conformably overlies the Yellowmans Creek Beds and is overlain by the Riversdale Volcanics with erosional disconformity, a relationship which may be seen in the SE of the area and has also been reported by Colquhoun (pers. comm.). It is dominated by sublitharenite, with subordinate quartzarenite, volclitharenite, conglomerate, lutite and accretionary lapilli tuff. The Roxburgh Formation has been presumed of ?Pragian age (Millsteed, pers. comm.) and this study cannot resolve the age of the Formation in the 'Glendale' area more precisely than Early Devonian.

Sublitharenites are the dominant lithology throughout the Formation and are characteristically fine- to medium-grained, cream to buff in colour, and either massive or more commonly displaying parallel-laminated bedding and low-angle tabular cross-bedding. They are typically quartz-cemented, submature, poor to moderately well-sorted and moderately close-packed, containing subrounded to subangular quartz, subrounded volcanic rock fragments, muscovite, rare K-feldspar and plagioclase grains, and traces of tourmaline, secondary sericite and chlorite.

A 2-3m thick pebble to cobble oligomictic conglomerate crops-out within the western sequence and is characterized by well-rounded dacite cobbles set in a matrix of subangular quartz, less common biotite, degraded plagioclase and abundant sericite and chlorite.

A 1-2m thick accretionary lapilli tuff horizon crops-out within the NE of the study area, providing a useful structural and stratigraphic marker near the base of the formation. Typically light brown to greenish in colour, the rock consists of abundant whole and fragmental accretionary lapilli, commonly cored by quartz anhedra, set in a fine-grained matrix.

In the western area there are a number of thin, fine-grained light coloured lutite horizons, probably representing volcanic ash deposits.

Fossiliferous shales and volclitharenites occur as common interbeds towards the top of the sequence. The litharenites contain an abundance of chloritized volcanic rock fragments. The shales are light brown in colour, prominently cleaved and contain the following fauna: *Calymene* sp. *Howellella* sp., *Iridistrophia* sp., *Leptaena* sp. and *?Delthyris* sp., as well as a number of corals, molluscs and bryozoans. In the upper western sequence massive- to poorly-bedded quartzarenite constitutes the uppermost unit of the Formation and contains limestone pebbles rich in crinoid ossicles and favositid corals.

A distinctive brachiopod fauna is developed near the base of the eastern sequence where extremely fine-grained sublitharenites are interbedded with shales containing large numbers of *Iridistrophia* sp., numerous bryozoans, favositids and carbonaceous plant remains.

The depositional environments of the Roxburgh Formation are defined by the occurrence of marine fossils, parallel-laminated bedding and low-angle cross-bedding, bioturbation and the accretionary lapilli horizon.

The lowest part of the sequence is restricted to quiet marine conditions with the accretionary lapilli horizon representing the manifestation of contemporaneous phreatomagmatic silicic volcanism. Abundant lapilli rinds imply limited reworking (Cas and Wright, 1987), but this must exclude vigorous wave action, suggesting the offshore transition zone of Reineck and Singh (1980). Higher in the sequence the sandstone becomes coarser and displays parallel-laminated bedding, low-angle tabular cross-bedding, small-scale ripples, bioturbation and pebbly horizons typical of the shoreface facies described by Reineck and Singh (1980). The uppermost western deposits of massive coarse sandstone represent upper to middle shoreface deposition, where limestone clasts from an unknown source have probably been ripped-up and redeposited by storm action.

The overall sequence is interpreted as a shallowing sequence where lower units represent deposition in the lower shoreface to transition zone (4-15m) which is overlain by lower to middle shoreface deposits (6-10m), in turn overlain by middle to upper shoreface deposits.

Riversdale Volcanics

The Riversdale Volcanics were proposed as the Riversdale Rhyolite by Wright (1966), and the name was modified by Offenberg *et al.* (1971). The Volcanics have been described by Pemberton (1980) and Millsteed (1985). The unit crops-out extensively within the 'Glendale' area and is represented by a much greater thickness than has hitherto been described. The Volcanics overlie the Roxburgh Formation with erosional disconformity; however, the erosional unconformity between the Riversdale Volcanics and the overlying Carwell Creek Formation reported by Millsteed (1985), was not observed within the 'Glendale' area. The total composite thickness of the Riversdale Volcanics, including discontinuous sandstone bodies, amounts to 1250m; however the maximum outcrop thickness is 890m. This differs from the 200m and 320m reported by Pemberton (1980) and Millsteed (pers. comm.) from areas to the W and N respectively.

Mapping within the 'Glendale' area has refined the stratigraphy of the Riversdale Volcanics, allowing recognition of seven mappable lithologies (Fig. 4); these are basal conglomerate, volcanic ash unit, three volclitharenite units, a sublitharenite unit and the dominant ignimbrite series, of at least five individual units. No lavas were found within the Riversdale Volcanics.

Basal Conglomerate

This poorly outcropping unit occurs at the base of the Volcanics, having its best exposure, and maximum thickness of 25m in the southeast of the study area. In the western portion of the study area the unit is very poorly developed, with a maximum thickness of 2m.

In the east the unit is a crudely bedded, matrix-supported, volcanilithic conglomerate, consisting of subrounded to subangular cobbles of rhyodacite set in volcanilithic sand matrix. There is patchy development of breccia horizons, with angular clasts up to 75cm in size. In the west the conglomerate is characterized by rounded sublitharenite clasts and subangular clasts of rhyodacite, supported in a fine lithic sand matrix.

Rounded sandstone clasts in the west suggest reworking of units of the Roxburgh Formation.

Volcanic Ash Unit

A fine-grained cream to pink coloured ash unit occurs near, or at the base of, the Riversdale Volcanics. At some localities the ash unit can be observed above the conglomerate, whereas at others the ash unit occupies a basal position on top of the Roxburgh Formation. It has a maximum thickness of 2m but is typically around 1m thick. Outcrop is poor but widespread. The ash unit is mostly composed of irresolvable fine grains, thought to be devitrified glass shards, displaying microbedding structures. Accretionary lapilli up to 12mm in diameter are common.

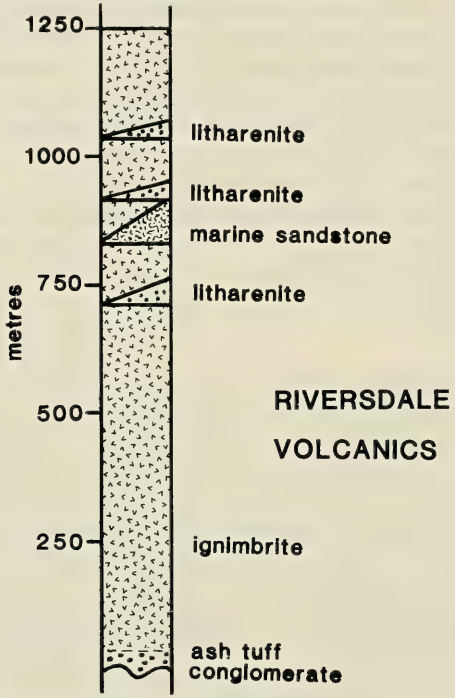

Fig. 4. Detailed stratigraphy of the Riversdale Volcanics.

Ignimbrite Series

The Riversdale Volcanics are mostly comprised of large thicknesses of ignimbrites; however, individual flow units cannot be positively identified, but they are at least 10m in thickness, as shown by the vertically continuous welding of more than 10m of sequence. These ignimbrites vary from hard, deep-purple, strongly welded tuff to somewhat weathered, grey-green, non-welded units, which have a distinctive jagged outcrop pattern. Commonly large stretched out fiamme are distinguishable in outcrop and hand specimen.

The ignimbrites consist of cognate rhyodacite fragments, flattened pumice lapilli, and abundant broken phenocrysts of quartz and feldspar, in a fine-grained dark groundmass. Rhyodacite fragments are up to 50mm in size, and are typically angular. Pumice lapilli, commonly replaced with carbonate and sericite show relict vesiculation and ragged wispy ends; they are difficult to distinguish from the groundmass in thin section and are best seen in weathered hand specimens, where they are up to 60mm long. Phenocrysts of quartz are fractured and embayed, everywhere anhedral and are up to 2mm in size. Subhedral to rare euhedral plagioclase (An = 7-10%) phenocrysts, up to 3mm are typically broken and display relict twinning and sporadic zoning.

Subordinate K-feldspar subhedra occur and are commonly twinned. Both feldspar phases are highly altered to sericite and carbonate. Trace opaque oxides occur sporadically.

The groundmass consists of devitrified glass shards or irresolvable fine ash. The shards appear as foliated and welded fragments showing alteration to microcrystalline quartz and feldspar, and whereas relict eutaxitic texture is obvious in welded samples, shards now show pin-point birefringence as a response to devitrification. Within non-welded samples the groundmass is exclusively fine ash.

Using the component criteria of Cas and Wright (1987), the ignimbrites are classified as welded vitric tuffs with subordinate non-welded vitric tuffs; their mineralogy suggests a rhyodacitic source. No textures suggestive of lavas were found within the sequence.

Arenite Units

Three discrete, large lenticular volcaniclastic bodies and a number of much smaller lenses occur within the Riversdale Volcanics. Individual units show great variation in thickness, and lens out over several hundred metres. In outcrop the units appear as medium- to coarse-grained, commonly pebbly, 'dirty' sandstones. Low-angle crossbeds are sometimes discernible in places. Volclitharenites are clast-supported, poorly sorted and immature. They contain angular to subrounded quartz, relict pumice lapilli, devitrified glassy fragments, feldspars and abundant volcanic clasts set in an extremely fine-grained groundmass representing devitrified ash. Carbonate is a common cement and alteration phase, as are chlorite, hematite and sericite.

A distinct thick, but lensoidal arenite unit is found within the Riversdale Volcanics, approximately two-thirds up into the sequence (Fig. 4). It differs markedly from other arenite units within the Volcanics in being cleaner. much lighter in colour, and massive to well-bedded. As it contains sporadic limestone pebbles, is bioturbated in places, and is far more quartzose than other arenites within this formation, it strongly resembles elements of the Roxburgh Formation; however, it contains far more volcanic detritus and is clearly conformable within the Volcanics. In thin-section it is a fine- to medium-grained, closely packed sublitharenite containing subangular to angular quartz, subrounded to subangular volcanic rock fragments and traces of muscovite, sericite, opaques and chlorite. Crinoid ossicles, an unidentified mollusc and the brachiopod *Iridistrophia* sp. were collected from this arenite unit.

Depositional Environment

The basal conglomerate and breccia beds of the Riversdale Volcanics suggest a slight to moderate reworking of volcanic and underlying detritus. The sparse distribution, variable thickness and the erosional contact suggest deposition of this unit in erosional hollows; however there are no identifiable trough structures to substantiate this view.

The presence of abundant whole accretionary lapilli within the ash unit negates extensive reworking of this unit. Such lapilli would be easily destroyed in water and, given the shallow environment of the upper Roxburgh Formation and the erosional base to the volcanics, this suggests subaerial deposition. The accretionary lapilli also indicate the presence of water vapour within the eruption column or storms associated with the eruption clouds (Cas and Wright, 1987).

Pemberton (1977, 1980) and Millsteed (1985) infer a subaquaeous environment for the Riversdale Volcanics on the basis that the underlying and overlying strata are shallow marine. Deposition of such thick welded ignimbrites would have filled and

exceeded the water depths of the shoreface environments of the Roxburgh Formation. Unless deposition of the units was accompanied by very rapid subsidence then, with commonly more than 10m of ignimbrite present, it is most likely that the ignimbrites are in the main subaerial. This conclusion is supported by the erosion surface and the nature of the ash layer. It is also supported by the abundance of welding textures throughout the Volcanics. Whilst welding can occur in shallow marine environments, it is generally only found in extremely shallow depths (Cas and Wright, 1987).

It is considered that steady subsidence continued throughout deposition of this formation, and that the marine sandstones are a result of this. Low-angle cross-bedding, and parallel laminated bedding, combined with limited bioturbation and the presence of limestone pebbles, suggest a shoreface environment for deposition of the sublitharenite unit. Above this unit thick ignimbrite deposition suggests further subaerial exposure.

The volclitharenite units within the Riversdale Volcanics offer little evidence for environmental interpretation. They are poorly-bedded and in places cross-bedded, and clast roundness suggests some reworking.

In summary, initiation of the Riversdale Volcanics began with the deposition of volcanically-derived conglomerates, overlain by a thin, probably subaerial ash fall unit. These were covered by an extensive sequence of subaerial silicic pyroclastic flows. Continual subsidence led to the deposition of a shallow-marine sand body during quiescence, and volclitharenite units accumulated between eruptive episodes from reworking of volcanic detritus.

Carwell Creek Formation

The Carwell Creek Formation crops-out extensively within the study area and consists of 280m of limestone, crinoid-rich sandstones, lithic sandstones and minor ignimbrite units. Originally defined as the Carwell Creek Beds (Offenberg *et al.*, 1971) the definition of a lower boundary (Pemberton, 1980; Millsteed, pers. comm.; and this work) and an upper stratigraphic boundary (Millsteed, pers. comm.) warrants the elevation of this unit to Formation status.

The basal part of the Carwell Creek Formation is characterized by a thin discontinuous impure limestone unit which has been informally named the 'Upper Kandos Limestone' (Cook, 1988; Pemberton, pers. comm.). The limestone attains a maximum thickness of 25m and is dominated by recrystallized microsparite and lesser pelsparite containing variable amounts of quartz grains (3-10%). Within northwestern exposures of the unit, the lithology is slightly more fossiliferous containing sporadic favositid and stromatoporoid fragments. Shale interbeds are exposed within disused quarries in the NW of the study area and fenestral textures to the limestone suggest intertidal exposure. The basal limestone is in part overlain by a distinctive sublitharenite unit which, at its base, is rich in crinoid ossicles. This variable lithology is mostly restricted to the central portions of the study area, and grades vertically into litharenite units which dominate the Carwell Creek Formation. Sedimentary structures within these units include tabular cross-bedding, planar bedding and rare pebbly lags, in addition to burrows. These crinoidal sandstones consist predominantly of fossil fragments, (decreasing in abundance with stratigraphic height), quartz grains and angular volcanic rock fragments cemented predominantly by ferroan-calcite with minor dolomite. The upper parts of this unit contain fewer crinoid fragments and are somewhat more quartz-rich.

Volcanic-rich sandstone beds dominate the Carwell Creek Formation, forming the bulk of the formation. These are poorly bedded, medium-grained, immature litharenites composed of abundant volcanic rock fragments, quartz grains and lesser

amounts of degraded feldspars. Tabular cross-beds are common, as are pebbly horizons. A thin, discontinuous, highly siliceous ignimbrite unit found in the uppermost Carwell Creek Formation is similar to unwelded tuffs described from the Riversdale Volcanics.

Low-angle tabular cross-beds and parallel-laminated beds suggest similar marine environments to those of the Roxburgh Formation. Carbonates were deposited in extremely shallow, possibly intertidal, shoals. Upper litharenite units provide little evidence for environmental interpretation. The upper ignimbrite highlights continuation of silicic volcanism during this time.

Depositional Sequence of Early Devonian Strata

The Early Devonian succession within the 'Glendale' area begins with the shallow, quiet, marine deposition of shale and fine sandstone of the Yellowmans Creek Beds. The lowermost Roxburgh Formation represents continuation of these conditions, eventually giving way to the coarser, shallower deposits which form the bulk of the Roxburgh Formation. Following an episode of erosion, evidenced by the erosional unconformity at the base of the Riversdale Volcanics, volcanic conglomerate heralded substantial silicic volcanic activity. The lower ash unit of the Riversdale Volcanics shows no evidence of substantial reworking, and subsequent ignimbrite deposition was probably subaerial. Minor shallow marine sublitharenites, are followed by continuation of ignimbrite deposits. A southerly source for the volcanics is indicated by a thinning of the Volcanics to the north, west and northeast (Pemberton, 1980: Millsteed, 1985; Colquhoun, pers. comm.). The transgressive Carwell Creek Formation was deposited in shoreface environments.

Significant hiatus and angular discordance between Early and Late Devonian units has been demonstrated by Millsteed (1985), but within the 'Glendale' area the boundary is faulted.

Late Devonian Strata

Late Devonian strata crop-out in a faulted block in the central north of the study area and consist of elements of the Buckaroo Conglomerate (Wright, 1966) and Bumberra Formation (Wright, 1966). Represented by a 150m thick unit, the Buckaroo Conglomerate consists of a coarse polymictic conglomerate, dominated by pebble- to cobble-sized, rounded clasts of quartzite, chert, quartz, volcanic and metamorphic rock fragments set in a sand-size quartz-lithic matrix. Its restricted exposure prevents accurate assessment of depositional environment; however, its coarse-grained rounded clasts supports Millsteed's (1985) view of fluvial deposition. The Late Devonian sequence is transgressive through a transitional series of mixed conglomerate-marine sandstone interbeds containing a sparse brachiopod fauna, to the marine Bumberra Formation. These units are quartz-rich, fine- to medium-grained sublitharenites, displaying parallel laminated bedding, shallowly-dipping tabular cross-beds and sporadic bioturbation. The Bumberra Formation is faulted against the Roxburgh Formation (Fig. 3).

Permian Strata

Essentially flat-lying Permian strata unconformably overlie the Devonian rocks in the south of the study area and are represented by 35m of Megalong Conglomerate, approximately 30m of Berry Siltstone and about 80m of Illawarra Coal Measures (Clarke, 1866). The Megalong Conglomerate (McElroy *et al.*, 1969) is a coarse cobble to boulder polymictic conglomerate, containing quartzite, chert, volcanic and polycrystal-

line quartz clasts set in a quartz-lithic matrix. Coarse sand horizons define broad trough structures, supporting the long-held view of a fluvial origin for the Megalong Conglomerate (Dulhunty and Packham, 1962). This is further evidenced by the irregularities in unit thickness, a response to the palaeorelief at the base of the unit. The Megalong Conglomerate is overlain by fine siltstones of the Berry Siltstone (David and Stonier, 1890), which contain common boulder erratics suggesting possible glacial rafting during deposition. The Illawarra Coal Measures commence with a light coloured oligomictic conglomerate, the Marrangaroo Conglomerate (Stephens, 1883), which is in turn overlain by poorly exposed, fine-grained siltstone, sandstones and shales forming the remainder of the incomplete section.

Structure

Devonian strata within the study area have been deformed into gentle upright synclines and anticlines which, in general, trend N-NW (330-350°) and plunge shallowly at 1-14°. A few major folds have shallow southerly plunging axes. All folds have upright axial surfaces and are asymmetrical with steeper limbs to the west. They are open with interlimb angles between 130 and 170°. The overall fold pattern defines a small synclinorial zone trending SE-NW with a plunge of 1-2° to NW. A representative cross-section through the area is given below (Fig. 5).

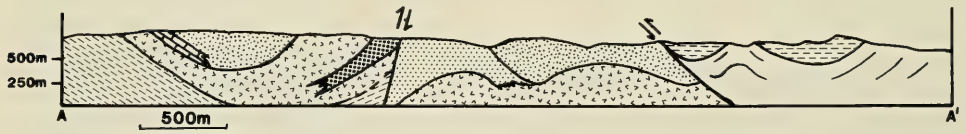

Fig. 5. Cross-section A-A[1] through study area. No vertical exaggeration. Legend as per Fig. 3, except Yellowmans Creek Beds (unshaded).

Mesoscopic folds are well developed in the well-bedded Yellowmans Creek Beds and Roxburgh Formation, possessing upright axial surfaces and rounded hinges, and are generally open with interlimb angles from 100-130°. They have no apparent asymmetry. In the NE of the area slightly more intense folding highlights the thinning of the Riversdale Volcanics and a well-developed, near-vertical axial planar cleavage is present, striking NW.

Three major faults occur in the 'Glendale' area. To the N of 'Glendale' farmhouse the Carwell Creek Formation is normally faulted against the Late Devonian Buckaroo Conglomerate. Millsteed (1985) interpreted this fault, to the immediate N to lie on the unconformity between Early and Late Devonian strata and as such represents some minor stratigraphic throw. To the immediate E, the Roxburgh Formation is thrust against the Bumberra Formation. Similarities of lithology between the Roxburgh Formation and the Bumberra Formation prevent accurate calculations of the displacement on this fault. It is clear, however, that there is some considerable strike slip component to both these faults. The third major fault extends from the NW of the study area, SE principally through the Riversdale Volcanics. To the W of 'Glendale' the fault is represented by an extensive cleavage zone through the Volcanics, whilst to the

immediate S of 'Glendale' the Riversdale Volcanics are thrust over the Carwell Creek Formation revealing a net stratigraphic displacement in the order of 100-200m.

The stratigraphic discontinuities of sandstone beds within the Riversdale Volcanics in the creek S of the farmhouse can be rationalized in terms of an extension of the Roxburgh Formation-Bumberra Formation thrust. Thus the central portion of the study area is seen as a fault slice. Unlike the other fault systems within the study area, which are expressed as a string of ironstone quarries defining brecciated zones, the latter is an inferred fault defined on the basis of stratigraphic discontinuities within the 'Glendale' valley. Minor cross cutting faults are common in the study area.

Geological History

The Capertee High had risen by the mid-Silurian (Jones *et al.*, 1987) in response to dextral transtension along the then eastern margin of the Lachlan Fold Belt (Powell, 1984).

Early Devonian strata within the 'Glendale' area represent continuation of deposition on the Capertee High, with initial deposition of shallow-marine shales and sandstones of the Yellowmans Creek Beds. Continuing shallow-marine deposition was coupled with manifestations of phreatomagmatic silicic volcanism, as evidenced by accretionary lapilli tuff within the Roxburgh Formation. Shallow-marine transition to shoreface conditions were responsible for the deposition of the Roxburgh Formation.

Following a period of subaerial exposure and erosion, the deposition of coarse volcaniclastics and volcanic ash heralded the substantial silicic volcanism of the Riversdale Volcanics; the resulting thicknesses of ignimbrite were deposited from a southerly source in a predominantly subaerial environment. Shallow-marine sandstones within the Volcanics represent minor transgressive marine influences during periods of quiescence. The Carwell Creek Formation was deposited in response to continued subsidence, again in a shallow-marine environment. Minor silicic volcanism continued to provide detritus and minor ignimbrite during deposition. Following the hiatus associated with mid-Devonian tectonic movements, as discussed by Powell and Edgecombe (1978) and Millsteed (1985), the Late Devonian Buckaroo Conglomerate was deposited in a fluvial environment. Further marine transgression resulted in the deposition of the Bumberra Formation. The Lawson's Creek Shale (Wright, 1966) is not present within the study area due to faulting, but has been identified by Millsteed (pers. comm.) to the immediate N.

Timing of the major deformation within the 'Glendale' area is post-Devonian, pre-Permian and is best attributable to the Kanimblan Deformation, as discussed by Powell *et al.* (1976), which has had such a profound effect on the northern Lachlan Fold Belt.

Permian strata represent deposition at the margins of the western Sydney Basin and show possible glacial influence at the base.

Acknowledgments

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Vascular Plants with Restricted Distributions in the Western Division of New South Wales

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(Communicated by J. R. MERRICK)

PRESSEY, R. L., COHN, J. S., & PORTER, J. L. Vascular plants with restricted distributions in the Western Division of New South Wales. *Proc. Linn. Soc. N.S.W.* 112 (2), 1990: 213-227.

Two hundred and thirty-nine plant taxa with restricted occurrences in the Western Division of New South Wales were identified to significantly enlarge the list of rare plants known from the region as a basis for a conservation strategy. Restricted plants were defined by compiling a preliminary list of taxa known or thought to be localized or sparsely distributed in the Western Division and by progressively refining this list with information from the literature, herbarium collections and botanists throughout south-eastern Australia. Distributional categories were based on overall national distribution. Six taxa are endemic to the region and a further five occur only in New South Wales. Two hundred and six taxa also occur interstate, although 73 of these appear to have small ranges and/or few occurrences throughout their ranges. Twenty-eight taxa have occurrences in the Division disjunct from their main populations. Regional conservation priorities for each taxon were identified from the extent to which the Western Division contains its total occurrences and from established Australia-wide priorities.

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KEY WORDS: Rare plant conservation, reserve selection.

INTRODUCTION

Research is under way by the National Parks and Wildlife Service and CSIRO to refine systematic procedures for selecting conservation reserves in New South Wales, with initial emphasis on the Western Division (Pressey and Nicholls, 1989a,b, 1990). The Western Division covers approximately 320,000 square kilometres of the semi-arid and arid parts of the state (Fig. 1). Reserve selection trials in this region have been based on land system mapping at 1:250,000 prepared by the Soil Conservation Service, the most detailed and consistent delineation of natural environments in the region. As a basis for biological conservation, land systems and other land classes like plant communities, soil types and geological units are surrogates for comprehensive data on the distribution and abundance of each species in a region. Such information on species could be used to ensure that all plants and animals were in declared or proposed reserves at the time of survey, although movements of fauna and the effects of temporal processes on reserved populations would still need to be addressed. However, these comprehensive data are considerably harder to obtain than maps of land classes and are unlikely to be complete before competition with other land uses forces pragmatic decisions on the locations and extent of the last reserves in many regions. Reservation on the basis of land classes will therefore continue to be a practical necessity.

Reservation of land classes alone cannot ensure, however, that all species are protected. Land classes are often heterogeneous entities in terms of species occurrence and other attributes (Beckett and Burrough, 1971; Pressey and Bedward, 1990). Many species are therefore likely to slip through the 'coarse-filter' of reservation based on land classes and will need to be protected with a 'fine-filter' or species-specific strategy (Noss, 1987; Hunter *et al.*, 1988). Others will be represented in reserves by very small proportions of their total populations. The species most likely to be missed or under-represented are the ones which are relatively rare. Many rare plant species are not

known to occur in conservation reserves. Of the 199 species of plants in the Victorian mallee which are rare or threatened in the state context, only 87 (44%) are known to occur in a conservation reserve (Cheal and Parkes, 1987). Of the 1115 rare or threatened species of plants in Queensland, 556 (50%) have been recorded from reserves in Queensland and only another seven are known from reserves interstate (Thomas and McDonald, 1987). Of the 3329 Rare or Threatened Australian Plants (ROTAP's) listed by Briggs and Leigh (1988), 1719 (53%) are known to occur in conservation reserves and only 328 (10%) are considered to be adequately reserved, even though many reserves have been dedicated specifically for rare and endangered plants in recent years.

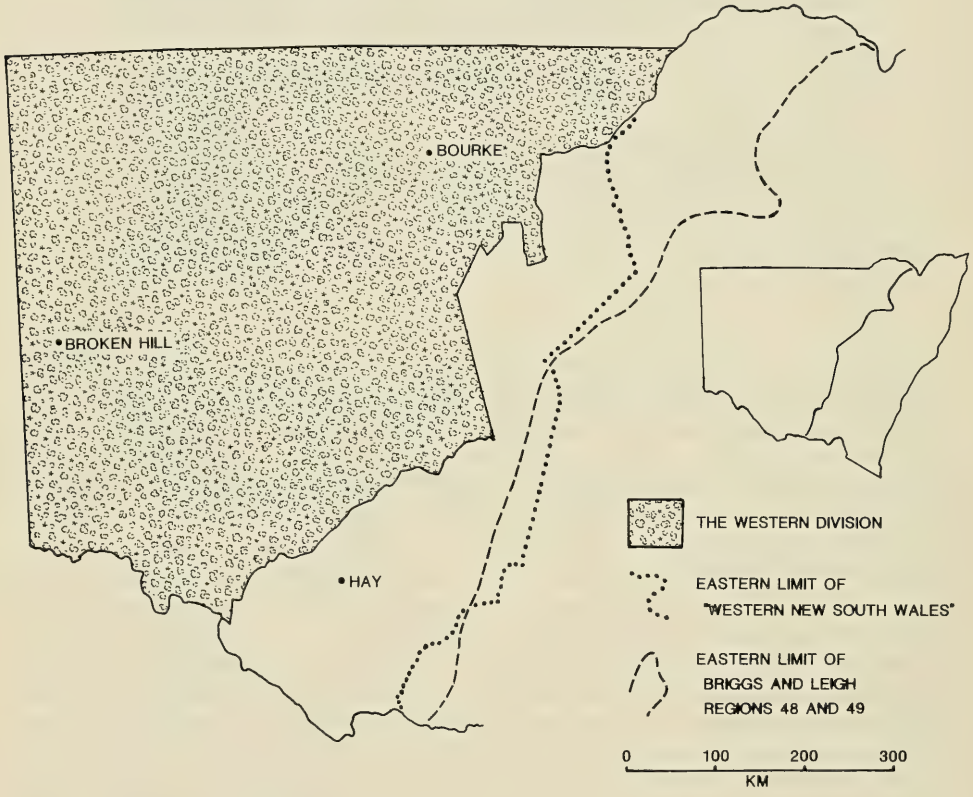

Fig. 1. The Western Division of New South Wales in relation to 'Western New South Wales' as defined by Cunningham *et al.* (1981) and the botanical regions used by Briggs and Leigh (1988).

In the absence of comprehensive data on the distribution and abundance of all the plants in a region and with limits on the area which can be dedicated to conservation, there are at least three ways of maximizing the number of plant species contained in reserves.

1. Reserves can be located to maximize the effectiveness of the 'coarse-filter' in reserving the biological diversity of a region. Possible approaches include focussing reserves on areas of high environmental diversity (Miller *et al.*, 1987).
2. Land classes can be replaced as a basis for reservation by the localities of rare species. Game and Peterken (1984) and Pressey and Nicholls (1989a) showed that reserving sites with rare species can be an effective way of protecting the total floristic diversity, although both analyses were based on comprehensive survey data. Reliance on *a priori* assessments of rare or threatened species might yield less impressive results. The success of this approach also depends on whether rare species are concentrated in one or a few of the environments in a region or scattered through many environments.
3. Land classes can be complemented as a basis for reservation with information on the locations of species least likely to occur in reserves selected solely according to land classes. This is only a partial solution to the limitations of land class reservation because there is no guarantee that the set of species so identified will be the same as that which slips through the 'coarse-filter'. More research is therefore needed to define the characteristics of species missed by land class reservation and to compare these with the criteria used to define lists of rare or threatened species.

The third approach is being taken by the National Parks and Wildlife Service in the Western Division because of its obvious, if probably incomplete, contribution to conserving the plant taxa of the region. Application of the other two approaches will await the results of further research on their potential value. For maximum effectiveness, the third approach requires a new compilation of information on plant species with restricted distributions in the Western Division. The recent assessment of rare or threatened plants in a national context (Briggs and Leigh, 1988) listed only 35 species which occur in the Western Division. Reserves based on land system mapping cannot be expected to adequately represent populations of all the other plant species in the Division, many of which occur in small and widely scattered localities. A broader assessment of species warranting particular attention is therefore needed to complement the 'coarse-filter' approach. Leigh *et al.* (1981) recognized the need for conservation of plant populations of special interest such as these, even though the taxa might be too common nationally to be listed as Rare or Threatened Australian Plants.

This paper describes the methodology for defining categories of distribution and priorities for conservation for restricted plant taxa in the Western Division, using considerably broader criteria than Briggs and Leigh (1988), and presents the results of the study.

Approaches to Defining Plant Species of Conservation Significance

Rare species are generally accorded special conservation significance because their small or scattered occurrences and low numbers of individuals render them unlikely to be protected, unless specifically targeted, and particularly liable to depletion or extinction from a variety of land uses. Several types of rarity can be distinguished on the basis of different combinations of geographical range, habitat specificity and local population size (Rabinowitz, 1981). Conservation significance has also been given to species, including widespread and common ones, in danger of depletion and to actual or presumed genetic variants which are disjunct from or peripheral to the main population of a species.

Plant species which are rare or otherwise of conservation significance have been defined in Australia using a variety of criteria and with varying levels of subjectivity.

The criteria fall into two broad classes, reflecting distribution and vulnerability, respectively.

Indicators of significance based on distribution include the absence of records since type collection (Specht *et al.*; 1974, Briggs and Leigh, 1988), the size of a species' range (Rye, 1982; Briggs and Leigh, 1988), number of sampling sites or grid blocks occupied (Pryor, 1981; Pickard, 1983; Binns, 1988), habitat specificity (Briggs and Leigh, 1988), endemism (Jessop, 1977; Brown *et al.*, 1983; Binns, 1988), disjunct occurrences (Specht *et al.*, 1974; Hartley and Leigh, 1979) and distributional limits (Binns, 1988; Mills, 1989). Abundance has been combined with distributional information by several authors to define rarity (Pickard 1983; Lang and Kraehenbuehl, 1987; Binns, 1988).

Subject to the limitations of collection localities as indicators of the actual occurrence of species, some of the distributional criteria lend themselves to objective appraisal. For example, collection localities were used by Rye (1982) and, for one category, by Briggs and Leigh (1988) to measure actual geographical range, by Pryor (1981) and Pickard (1983) to indicate number of grid blocks occupied and by Binns (1988) to identify limits of distribution. Other definitions of rarity have been more subjective, especially those which involve habitat specificity or abundance, which are usually difficult to quantify, but also some dealing with geographical range. Category 3 of Briggs and Leigh (1988) refers to 'species with a range over 100km in Australia but occurring only in small populations which are mainly restricted to highly specific and localized habitats'. Lang and Kraehenbuehl (1987) referred to uncommon species as 'relatively restricted or infrequent but more abundant than 'rare' . . .'. They defined 'rare' species, after Briggs and Leigh (1988), as those which 'may be represented by a relatlvely large population in a very restricted area or by smaller populations spread over a wider range'. Estimates of abundance have also been largely subjective.

Disjunct occurrences are difficult to identify consistently, even with locality data, because of differences in the geographical range, density and separation of groups of records representing discrete populations. Even when outlying populations are delineated, there remains the problem of different and often unknown dispersal abilities of species which determine whether a population is genetically as well as geographically isolated. In addition, judgement is necessary as to whether the outlying record is a sporadic occurrence of no long-term consequence or a persistent, viable population. Chippendale and Wolf (1981) used objective, although arbitrary, criteria to define levels of disjunction in *Eucalyptus*. Subjectively defined disjunct occurrences were listed by Specht *et al.* (1974) and Hartley and Leigh (1979).

Assessments of vulnerability have been used alone or in combination with distributional criteria to indicate conservation significance. Vulnerability has been based on representation in conservation reserves (Brown *et al.*, 1983; Briggs and Leigh, 1988), land tenure (Pryor, 1981) and general appraisals of the impacts and threats of land use (Specht *et al.*, 1974; Lang and Kraehenbuehl, 1987; Briggs and Leigh, 1988; Gullan *et al.*, 1990).

Collection localities have also been used to indicate vulnerability, for example by Pryor (1981) and Brown *et al.* (1983). However, a general assessment of vulnerability requires information other than occurrence on land of specified tenure and management. The survival of all reserved species is by no means assured and threats to unreserved species vary widely in nature and severity. Unavoidably, the determination of degree of threat is highly subjective. The 'endangered' and 'vulnerable' categories of Briggs and Leigh (1988), applied by others in state contexts, rely on judgements of how long before the species will disappear from the wild if threats continue or whether populations will be affected by changes in land use. Gullan *et al.* (1990) added a 'depleted'

category for their Victorian assessment to indicate species which may be common or widespread but are declining due to lack of regeneration.

Internationally, an important influence on the identification of plant species of special conservation significance has been the Red Data Book 'status' (vulnerability) classification of the International Union for the Conservation of Nature (IUCN) Threatened Plants Committee, described by Lucas and Synge (1978) and others. The binary coding for ROTAP's incorporates the IUCN 'status' categories which are gaining acceptance world-wide, although major differences in national lists still remain (Leigh *et al.*, 1981).

Methods and Categories

Of the two major considerations in assessing the conservation significance of plant taxa — distribution and vulnerability — only distribution was used in this study. Regional distribution will be a major determinant of the occurrence of taxa in reserves selected to represent land classes in the Western Division. Overall national distribution also has a bearing on the consequences and urgency of conservation measures in any particular region. The importance of assessing vulnerability separately from distribution is acknowledged but such an assessment, ideally covering both threat and the biological reasons for conservation risk, was beyond the scope of this project. The occurrence of species in Western Division reserves could have been dealt with inconsistently with existing information but a thorough treatment requires a systematic analysis of locality data for each species and, preferably, considerable new field work, both of which demanded resources not available for this study.

There are approximately 1600 native plant taxa in the Western Division and only a very small proportion of records has been computerized at the three major herbaria housing material from New South Wales — the National Herbarium of New South Wales, the Australian National Herbarium and the Australian National Botanic Gardens. Because of the consequent difficulty of basing this study on collection localities and because of the limited published information on habitat specificity and abundance, distributional criteria were assessed subjectively, relying on the judgement of taxonomists and field botanists. Disjunct occurrences were identified, but no assessment was made of their genetic significance or chances of persistence. Limits of distribution were not considered because there appears to be no single major directional trend in the geographical ranges of plant taxa in the Western Division.

The study covered species and infraspecific taxa. One broad class of plant taxa was identified: those with an overall distribution or disjunct occurrences so restricted that they could be absent or under-represented in a reserve system selected by the 'coarse-filter' approach. The term 'restricted distribution' is used here to indicate a small total range or a larger range consisting of relatively few localized occurrences. This definition is necessarily subjective, but no more so than in several recent state and national assessments of rare or threatened plants. Disjunct occurrences were defined as those which are localized and widely separated from a more extensive cluster of records representing the main population.

The identification of plant species with restricted distributions in the Western Division proceeded in a series of steps.

1. A preliminary list for comment by botanists was compiled mainly from the information on distribution and habitat of plants in western New South Wales given by Cunningham *et al.* (1981). The region defined by these authors was somewhat larger than the Western Division (Fig. 1). Taxa were included on the list if there was any suggestion of localized, marginal or disjunct occurrences in the Western Division,

regardless of their distributions elsewhere. Species listed as ROTAP's by Briggs and Leigh (1988) in their regions 48 and 49 were also included. The preliminary list consisted of 415 taxa. Further reduction initially would have pre-empted the judgement of experts on the region or on particular plant groups.

2. The preliminary list was sent for comment to field ecologists with extensive knowledge of western New South Wales or neighbouring interstate areas and to taxonomists working on each of the families in Adelaide, Brisbane, Canberra, Hobart, Melbourne and Sydney. Given the rationale for the study, the botanists were asked to indicate which taxa on the preliminary list or which additional taxa occurring in the Western Division warranted specific conservation efforts according to the four criteria listed below:
   (i) occurring only in the Western Division and only with localized occurrences;
   (ii) localized in the Western Division and throughout their ranges elsewhere;
   (iii) having marginal and localized occurrences in the Western Division and being depleted or threatened elsewhere (in practice, vulnerability elsewhere could only be judged with any consistency on the basis of range and number of records);
   (iv) having disjunct occurrences in the Western Division.
3. While the preliminary list was being considered by botanists, the status of Western Division plants nationally and in neighbouring states was checked using information from Thomas and McDonald (1987) for Queensland, Lang and Kraehenbuehl (1987) for South Australia and Gullan *et al.* (1990) for Victoria. Rare, threatened or extinct status in one of these publications gave greater significance to taxa not on the preliminary list for the Western Division and these were reconsidered for inclusion, subject to information on their distribution and abundance in New South Wales and the other neighbouring states.
4. The information from Steps 2 and 3 was compiled by recording rare, threatened or extinct ratings from the interstate references and all comments from experts for each taxon on the expanded list. To this compilation was added information on distribution and status from all relevant identification guides and taxonomic literature. Each taxon was then assessed to decide whether it should be left on or deleted from the list or had uncertain significance because of insufficient or conflicting information. It was also decided to broaden the criteria for inclusion on the list. Taxa were added if they had only localized occurrences in the Western Division but were widely distributed and/or common in other states. These are plants which New South Wales has a responsibility to conserve within its borders, even if they are given relatively low priority, because their conservation is not necessarily assured interstate and occurrences in this state could often represent genetic variants of the overall population. These taxa were easily identified from the information compiled.
5. Additional information needed to decide on taxa with uncertain significance was identified and specific questions were addressed to the most appropriate taxonomists or field ecologists.
6. Following the second responses from botanists, any outstanding queries were considered by checking the localities of specimens at the National Herbarium of New South Wales and by further reference to the literature, including the unpublished updates of Jacobs and Pickard (1981) and Jacobs and Lapinpuro (1986) at the National Herbarium of New South Wales. This step also involved an attempt to make the inevitably subjective judgements of disjunct occurrences as consistent as possible. All taxa thought to have disjunct occurrences on the preliminary list, those

indicated by experts as being disjunct and Western Division species listed by Specht *et al.* (1974) and Hartley and Leigh (1979) as disjunct were reviewed. Queries were resolved by reference to the literature and to specimens at the New South Wales herbarium.

This process allowed taxa with restricted distributions in the Western Division to be placed in six final categories and sub-categories according to their overall national distribution. The categories (listed below) were designed to indicate the degree to which protection of taxa in the Western Division, and in New South Wales, could influence their overall conservation.

CATEGORY 1: Occurring only in the Western Division with a restricted distribution.
CATEGORY 2: Occurring only in New South Wales with a restricted distribution within and outside the Western Division.
CATEGORY 3: Restricted distribution in the Western Division and also occurring interstate:
(A) small range and/or few records interstate;
(B) wide range and/or many records interstate.
CATEGORY4: Disjunct occurrences in the Western Division (widely dispersed localized occurrences are covered by categories 2 and 3A).
(A) main population interstate;
(B) main population or a significant part of main population in New South Wales.

Results and Discussion

The list of restricted plants contains 239 taxa of which 34 are subspecies, varieties or forms (Appendix). One of the listed taxa is a fern, 32 are monocotyledons and 206 are dicotyledons. Fifty-three families are represented on the list: one from the ferns, eight from the monocots and 44 from the dicots. Families with the highest numbers of listed taxa are Fabaceae (39), Chenopodiaceae (30), Asteraceae (28) and Poaceae (16).

The distribution of taxa between categories is shown in Table 1. Six taxa occur only in the Western Division and only in restricted localities (Category 1). Another five also occur elsewhere in New South Wales, but not interstate, and only in small areas throughout (Category 2). Some 206 taxa (86% of all taxa on the list) have restricted distributions in the Western Division but also occur interstate. Seventy-three of these (31% of list) appear to have small ranges and/or sparse distributions interstate (Category 3A) while the other 133 (56% of list) appear to be widely distributed and to have many collection localities interstate (Category 3B). Twenty-eight taxa (12% of list) have disjunct occurrences in the Western Division. In 19 cases, the main population is interstate (Category 4A). Another nine have at least a significant proportion of their occurrences in New South Wales (Category 4B).

Six taxa, including two ROTAP's, were each placed in two categories: 4A combined with either 3A or 3B. Category 4A is generally a special case of Category 3B, i.e. taxa widely distributed interstate but with one or more disjunct, not just localized, occurrences in the Western Division. The three taxa placed in both Categories 3B and 4A each have two types of restricted occurrences in the Western Division: one or more relatively continuous with the main distribution and one widely separate. Category 4A combined with 3A indicates that an occurrence in the Western Division is relatively widely separated from a few, scattered records interstate.

Briggs and Leigh (1988) listed 51 species of ROTAP's in their regions 48 and 49 which cover an area of western New South Wales somewhat larger than the Western

Division (Fig. 1). Of these, 33 are listed here as restricted in the Western Division. Sixteen were found not to occur in the Western Division following checks of herbarium specimens and advice from taxonomists. The other two were found to be too widely distributed to fit the categories used in the present study and therefore require reassessment as ROTAP's. *Echinochloa inundata* (Poaceae) is relatively common in parts of New South Wales to the east of the Western Division (S. Jacobs, pers. comm., 1990) and has been frequently collected (Vickery, 1975). Material for *Tribulus* (Zygophyllaceae) has recently been revised for the Flora of New South Wales and *T. minutus* found not to be rare or threatened and to occur mainly on the slopes and plains to the east of the Western Division (K. Wilson, pers. comm., 1990). Both these species were listed by Briggs and Leigh (1988) as having poorly known status (vulnerability).

TABLE 1

Distribution of taxa between categories

Category	No. taxa	% Taxa	ROTAP's#
1	6	3	3
2	5	2	3
3A	73	31	27
3B	133	56	
4A	19	8	2
4B	9	4	
	245(239)*	104(100)*	35(33)@

Rare or Threatened Australian Plants listed by Briggs and Leigh (1988);
* Six taxa were each placed in two categories;
@ Two taxa were each placed in two categories.

Two taxa endemic to the Western Division and with very localized occurrences in the region should be added to the ROTAP list: *Atriplex infrequens* (Chenopodiaceae) and *Bertya* sp.A (Euphorbiaceae).

The distributional categories used for restricted plants in the Western Division allow the taxa on the list to be given priorities for protection. The priorities outlined below are intended to reflect the relative importance for national conservation of protecting taxa in the Western Division. The priority for each taxon is therefore based on the extent to which the Western Division contains its total occurrences and on the Australia-wide conservation categories of Briggs and Leigh (1988). Where taxa occur in two categories of different priorities, they have been given the higher of the two priorities. Priorities for the conservation of each taxon in the Western Division are listed in the Appendix.

PRIORITY 1. Category 1 and one taxon presumed extinct outside the Western Division (seven taxa): protection measures in the Western Division will completely determine the survival of these taxa nationally.

PRIORITY 2. All ROTAP's apart from those with highest priority (29 taxa): the rarity of and/or threat to these taxa throughout their ranges is confirmed or suspected and their conservation significance recognized in a national context. Protection measures in the Western Division will be a very important contribution to their conservation throughout Australia.

Seven of the taxa listed under priority 2 are presumed extinct in the Western Division, although they all occur interstate as well. Their national significance

warrants more searches of collection sites, if not destroyed, and of likely suitable habitat elsewhere.

PRIORITY 3. Categories 2 and 3A, excluding ROTAP's (49 taxa): these taxa have small ranges or only scattered occurrences elsewhere in New South Wales or interstate, although they are not as rare or threatened as ROTAP's. Their conservation in the Western Division will influence their overall survival. New South Wales agencies have sole responsibility for those taxa in Category 2.

One taxon with this priority, *Casuarina obesa*, is presumed extinct in the Western Division. Although not given ROTAP status, its few populations in south-eastern Australia are small and widely scattered and several are under threat.

PRIORITY 4. Categories 3B, 4A and 4B, excluding ROTAP's (154 taxa): protection in the Western Division is desirable to conserve the genetic variation within the ranges of these taxa and, for those in categories 3B and 4A, will be important for their continued existence in New South Wales. In addition, the extent of reservation of many of these taxa interstate or elsewhere in the Western Division or New South Wales is uncertain.

Both the distributional categories and priorities presented here have limitations which must be borne in mind in interpreting and using the results. These limitations apply, in varying degrees, to most compilations of rare or threatened plants:

- the survey effort in the region has been uneven, depending on land tenure, road access and distance from towns — this could have underestimated the distribution of some taxa;
- some taxa are inconspicuous or hard to identify when not flowering or fruiting or when affected by drought or grazing — these might be more extensive and abundant than indicated here;
- some taxa have large temporal variations in abundance in response to fire, rain and other factors — the apparent distribution of these plants depends on the timing of observations relative to bursts of recruitment and subsequent decline in numbers;
- herbarium records can overstate distribution and abundance in cases where species are declining because the total set of records largely reflects a more favourable historical situation;
- differences in the amount of taxonomic work between groups could have influenced the number of component taxa considered to have restricted distributions;
- subjective categories for distribution are likely to lead to some differences in interpretation between respondents;
- the availability and type of distribution maps has an influence on perceptions of distribution and therefore on the identification of taxa as restricted or disjunct.

The problems due to collecting inconsistencies and the limitations of herbarium specimens are offset to some extent in the present study by the reliance on the judgement of taxonomists familiar with particular groups and on the experience of field botanists. All the problems except taxonomic inconsistencies are minimized in studies such as that of Gullan *et al.* (1990) which are based largely on comprehensive field work, not possible for the present exercise.

A full picture of the conservation needs of plants in the Western Division requires information on both pattern and process in rarity and vulnerability. This study has contributed to the knowledge of the pattern of rarity and has prepared the way for a compilation of the collection localities of the taxa listed, a much less daunting task than

an analysis of the localities of each of the approximately 1600 native taxa in the Western Division. In the same way, existing compilations of rare plants provided a short list of taxa for the quantitative investigations of geographic range by Rye (1982). Locality data, as well as being essential if previously recorded occurrences of the listed taxa are to be protected, will allow verification of the results presented here and a consistent assessment of their coverage by reserves. The other part of the picture — the trends and causes of rarity and threat in the Western Division — is necessary to complement the spatial analysis presented here and requires considerable further work. This information could alter the priorities for protection to some extent. For example, some relatively widespread taxa might occupy habitats under threat from clearing or might not be regenerating effectively. The temporal perspective is also necessary if appropriate protection measures and research needs are to be formulated.

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APPENDIX

Plant taxa with restricted distributions in the Western Division

See text for definition of categories and priorities; bracketed figures beside family names indicate number of taxa listed for family; # indicates Rare or Threatened Australian Plants (Briggs and Leigh, 1988) and refers only to species, not to listed subspecies; (X) indicates presumed extinct in the Western Division; (+) indicates presumed extinct interstate; * indicates that notes are given on the status of the taxon at the end of the appendix. Authorities for plant names are those in Jacobs and Pickard (1981) as amended by Jacobs and Lapinpuro (1986), unless otherwise indicated.

Taxon	Cat.	Prior.
PTERIDOPHYTES		
ADIANTACEAE (1)		
Cheilanthes lasiophylla Pichi-Sermolli	3B	4
ANGIOSPERMS		
Monocotyledons		
COMMELINACEAE (1)		
Commelina ensifolia	3B	4
CYPERACEAE (5)		
#Eleocharis obicis	2	2
Gahnia lanigera	3B	4
Schoenoplectus laevis	3B	4
S. pungens	3B	4
Schoenus latelaminatus	3B	4
ERIOCAULACEAE (2)		
#Eriocaulon australasicum	3A(X)	2
#E. carsonii	3A	2
ORCHIDACEAE (5)		
Caladenia dilatata var. *concinna*	3A	3
C. filamentosa var. *tentaculata*	3B	4
Diuris cuneata Fitzg.	3A	3
Prasophyllum campestre R. Bates ined.	3A	3
#Pterostylis cobarensis M. Clements*	2	2
POACEAE (16)		
Aristida leptopoda	3B	4
A. longicollis	4A	4
A. muricata	3A	3
#Bothriochloa biloba	3A	2
#Echinochloa lacunaria	3A(+)	1
E. turneriana	3B	4
Elytrophorus spicatus	3B	4
Enneapogon intermedius	3B	4
Eragrostis falcata	3B	4
E. speciosa	3B	4
Paspalidium clementii	3B	4
Poa fax	3B	4
#Stipa metatoris J. Everett & S. W. L. Jacobs	3A	2
#S. nullanulla J. Everett & S. W. L. Jacobs	3A	2
Triodia basedowii	3B	4
T. mitchellii var. *pubivagina*	3A	3
PONTEDERIACEAE (1)		
Monochoria cyanea	3B	4
XANTHORRHOEACEAE (1)		
#Lomandra Patens	3A	2
ZANICHELLIACEAE (1)		
Lepilaena bilocularis	3B	4
Dicotyledons		
ACANTHACEAE (3)		
Dipteracanthus australasicus F. Muell. ssp. *australasicus*	3B	4
#Rhaphidospora bonneyana (F. Muell.) R. M. Barker	3A(X)	2
#Xerothamnella parvifolia	3A	2
AIZOACEAE (6)		
Glinus oppositifolia	3B	4
#G. orygioides	3A	2
Gunniopsis papillata	3B	4
Tetragonia eremaea	3B	4
Zaleya galericulata ssp. *galericulata*	3B	4
ssp. *australis* (Melville) S. W. L. Jacobs	4B	4
AMARANTHACEAE (4)		
Amaranthus grandiflorus	3B	4
Ptilotus latifolius	3B	4
P. parvifolius var. *laetus*	3B	4
P. polystachyus var. *polystachyus* f. *rubiflorus*	3B	4
APIACEAE (4)		
Actinotus paddisonii	3A	3
#Hydrocotyle sp.1 (Byrock)*	1	1
Trachymene ochracea	4B	4

APPENDIX Cont'd.

Taxon	Cat.	Prior.
Uldinia ceratocarpa	3B	4
ASTERACEAE (28)		
#Acanthocladium dockeri	3A(X)	2
Brachycome exilis	3B	4
#B. papillosa	2	2
Ceratogyne obionoides	3B	4
Cratystylis conocephala	3B	4
Dichromochlamys dentatifolia	3A	3
Erodiophyllum elderi	3B	4
Gnephosis skirrophora	3B	4
Helichrysum diotophyllum	3A	3
H. podolepideum	3B	4
Helipterum tietkensii	3B	4
H. troedelii var. *patens*	3A	3
Ixiochlamys nana	3B	4
Kippistia suaedifolia	3B	4
Leptorhynchos waitzia	3B	4
Olearia calcarea	3B	4
Pluchea baccharoides	3A	3
P. dentex	3B,4A	4
P. tetranthera	3B	4
Podotheca angustifolia	3B	4
#Senecio behrianus	3A(X)	2
S. murrayanus Wawra	3B	4
#Stemmacantha australis (Gaudich.) Dittrich*	3A	2
Streptoglossa adscendens (Benth.) Dunlop	3B	4
S. liatroides (Turcz.) Dunlop	3B	4
Vittadinia arida	3A	3
V. australasica (Turcz.) N. Burbidge var. *australasica*	3B	4
Waitzia citrina	3B	4
BRASSICACEAE (9)		
Blennodia canescens	3B	4
Cuphonotus andreanus	3A	3
C. humistratus	2	3
#Lepidium monoplocoides	3A	2
Menkea australis	3B	4
Pachymitus cardaminoides	3B	4
#Phlegmatospermum eremaeum	3A(X)	2
Rorippa eustylis	3B	4
Stenopetalum velutinum	3B	4
CAMPANULACEAE (2)		
Wahlenbergia aridicola P. J. Smith	3A	3
W. queenslandica Carolin ex P. J. Smith	3B	4
CAPPARIDACEAE (2)		
Capparis loranthifolia var. *loranthifolia*	3B	4
Cleome viscosa	3B	4
CARYOPHYLLACEAE (1)		
Polycarpaea spirostylis ssp. *glabra*	3B	4
CASUARINACEAE (1)		
Casuarina obesa	3A(X)	3
CHENOPODIACEAE (30)		
Atriplex acutiloba	3B	4
A. infrequens Paul G. Wilson	1	1
A. lobativalvis	3B	4
#A. morrisii	3A	2
A. nummularia ssp. *omissa* Aellen	3A	3
A. papillata	3A	3
A. quinii	3B	4
A. rhagodioides	3A	3
A. turbinata	3B	4
A. vesicaria		
ssp. *vesicaria*	1	1
ssp. *calcicola* Parr-Smith	4A	4
ssp. *macrocystidia* Parr-Smith	4A	4
ssp. *minor* (Aellen) Parr-Smith	3A	3
ssp. *sphaerocarpa* Parr-Smith	3A	3
ssp. *variabilis* Parr-Smith	4A	4
Dysphania kalpari Paul G. Wilson	3B	4
D. littoralis	4A	4
D. plantaginella	4A	4
D. platycarpa Paul G. Wilson	3B	4
D. rhadinostachya (F. Muell.) A. J. Scott ssp. *inflata* (Aellen) Paul G. Wilson	4A	4
D. simulans	3B	4
#Maireana cheelii	3A,4A	2
M. lanosa	3B	4
Osteocarpum pentapterum (F. Muell. & Tate) Volkens	4A	4
O. scleropterum (F. Muell.) Volkens	3A	3
Pachycornia triandra	3B,4A	4
Sclerolaena blackiana	3A	3
S. constricta	3B	4
S. limbata	3B	4

APPENDIX Cont'd.

Taxon	Cat.	Prior.
Threlkeldia inchoata	3B	4
CHLOANTHACEAE (1)		
Dicrastylis lewellinii	3B	4
CONVOLVULACEAE (2)		
Ipomoea diamantinensis	3B	4
Porana commixta Staples	4A	4
DROSERACEAE (1)		
Drosera indica	4A	4
ELATINACEAE (1)		
Bergia ammannioides Heyne ex Roth	3B	4
EUPHORBIACEAE (6)		
Bertya sp. A	1	1
Chamaesyce australis (Boiss.) Hassall	3B	4
Croton phebalioides	3A	3
#Euphorbia sarcostemmoides	3A(X)	2
E. stevenii	3B	4
Monotaxis macrophylla	3A	3
FABACEAE (40)		
Caesalpinioideae		
Senna sp. *(Cassia pruinosa)*	3B	4
Lysiphyllum gilvum	3B	4
Faboideae		
Crotalaria cunninghamii	3B	4
Desmodium campylocaulon	3B	4
Indigofera basedowii ssp. *longibractea* (J. M. Black) Peter G. Wilson	3A	3
I. brevidens	3A	3
I. helmsii Peter G. Wilson	3A	3
I. leucotricha	3B	4
Jacksonia turneriana	3B	4
Kennedia procurrens	3A	3
Muelleranthus trifoliolatus	4A	4
Psoralea graveolens	3B	4
Ptychosema anomalum	3A	3
Swainsona colutoides F. Muell.	3B	4
S. flavicarinata	3B	4
#S. laxa	3A	2
#S. microcalyx ssp. *adenophylla*	3A,4A	2
#S. murrayana	3A	2
S. oligophylla	3B	4
S. oliveri	3B	4
S. oroboides ssp. *reticulata*	4B	4
ssp. *sericea*	4B	4
S. rigida	3A	3
S. similis J. Thompson	3A	3
S. stipularis var. *purpurea*	3B	4
var. *longialata*	3B	4
#S. viridis	3A	2
Templetonia sulcata	3B	4
Mimosoideae		
Acacia acanthoclada	3B	4
A. calamifolia	4B	4
#A. carnei	3A	2
A. coriacea	3B	4
#A. curranii	3A	2
A. jennerae	3B	4
A. johnsonii	3B	4
A. notabilis	3B	4
A. petraea Pedley	3A	3
A. pycnantha	4B	4
A. rivalis	3A	3
FRANKENIACEAE (1)		
Frankenia crispa	3A	3
GOODENIACEAE (4)		
Goodenia berardiana (Gaudich.) Carolin	3B	4
G. occidentalis Carolin	3B	4
Scaevola parvifolia F. Muell. ex Benth.	4A	4
Velleia arguta	3A	3
GYROSTEMONACEAE (2)		
#Codonocarpus pyramidalis	3A(X)	2
Gyrostemon australasicus	3A	3
HALORAGACEAE (1)		
Myriophyllum striatum Orchard	3A	3
LAMIACEAE (1)		
Prostanthera ringens Benth.	3A	3
LENTIBULARIACEAE (2)		
Utricularia aurea	4B	4
U. dichotoma	4B	4
LOGANIACEAE (1)		
Mitrasacme paradoxa	3B	4
LORANTHACEAE (1)		
Amyema maidenii ssp. *angustifolium*	3A	3
MALVACEAE (7)		
Abutilon calliphyllum	3B	4
A. cryptopetalum	3B	4
A. macrum	3B	4
A. malvifolium	3B	4
Lawrencia squamata Nees	3B	4
Sida rohlenae	3B	4
S. sp. C (aff. *corrugata*)	3B	4
MYOPORACEAE (1)		
Eremophila bowmanii var. *latifolia*	3B	4

APPENDIX Cont'd.

Taxon	Cat.	Prior.
MYRTACEAE (7)		
Calytrix longiflora	3B	4
Eucalyptus gillii	3A	3
E. dolichocarpa D. J. Carr & S G. M. Carr	3B	4
E. porosa	3B	4
Kunzea ambigua	4B	4
Melaleuca glomerata	3B	4
Micromyrtus hexamera	3B	4
OROBANCHACEAE (1)		
Orobanche australiana	3B	4
POLYGALACEAE (3)		
Comesperma integerrimum	3B	4
C. scoparium	3B	4
Polygala linariifolia	3B	4
POLYGONACEAE (1)		
Muehlenbeckia diclina	3B	4
PORTULACACEAE (3)		
Anacampseros australiana	3B	4
Calandrinia disperma	3A	3
C. volubilis	3A	3
PROTEACEAE (6)		
Grevillea albiflora	3B	4
#G. kennedyana	1	1
G. nematophylla	3B	4
G. pterosperma	3B	4
Hakea ednieana	3A,4A	3
H. eyreana	3B	4
RHAMNACEAE (1)		
Pomaderris oraria	3B	4
RUBIACEAE (2)		
Oldenlandia galioides	3B	4
Opercularia turpis	3B	4
RUTACEAE (5)		
Boronia caerulescens	3B	4
Eriostemon brevifolius	3B	4
E. myoporoides ssp. *acutus*	2	3
#Phebalium obcordatum	3A	2
P. squamulosum ssp. *parviflorum*	3A	3
SANTALACEAE (3)		
Choretrum glomeratum	3B	4
Exocarpos sparteus	3B,4A	4
Santalum murrayanum	3B	4
SAPINDACEAE (1)		
Dodonaea microzyga var. *microzyga*	3B	4
SCROPHULARIACEAE (2)		
Elacholoma hornii	3A	3
Glossostigma drummondii Benth.	4A	4
SOLANACEAE (1)		
Nicotianz occidentalis ssp. *obliqua*	3B	4
#Solanum karsense	1	1
STACKHOUSIACEAE (2)		
Macgregoria racemigera	3B	4
Stackhousia clementii Domin	3B	4
THYMELAEACEAE (4)		
Pimelea elongata	3A	3
P. penicillaris	3A	3
P. serpyllifolia	3B	4
P. simplex ssp. *continua*	3B	4
TREMANDRACEAE (1)		
Tetratheca pilosa ssp. *pilosa*	3B	4
ZYGOPHYLLACEAE (1)		
#Zygophyllum humillimum	3A	2

* *Pterostylis cobarensis* (Orchidaceae): listed by Briggs and Leigh (1988) as *Pterostylis* sp. 4 (Cobar district).
* *Hydrocotyle* sp. 1 (Byrock) (Apiaceae): as listed by Briggs and Leigh (1988); under revision by H. Eichler at the Australian National Herbarium.
* *Stemmacantha australis* (Asteraceae): listed by Briggs and Leigh (1988) as *Rhaponticum australis*.

Morphological, Ultrastructural and Physiological Characteristics of Damage to an Extensive Stand of the Lichen *Usnea sphacelata* at Casey Station, East Antarctica

ERICA ADAMSON, HEATHER ADAMSON, MARET VESK and RODNEY D. SEPPELT

ADAMSON, E., ADAMSON, H., VESK, M. & SEPPELT, R. D. Morphological, ultrastructural and physiological characteristics of damage to an extensive stand of the lichen *Usnea sphacelata* at Casey Station, East Antarctica. *Proc. Linn. Soc. N.S.W.* 112 (4), 1990: 229-240.

An extensive stand of the foliose lichen, *Usnea sphacelata*, in the immediate vicinity of the new Casey Station (lat. 66°17′S, long. 110°32′E), East Antarctica, displays unusual symptoms of severe damage, the cause of which is unknown. The heavily pigmented upper sections of the thallus are absent giving it the appearance of having been uniformly shaved and the remnant tips are frequently bleached with the central strand often protruding beyond the remaining medulla and outer cortex. Where damage has occurred well above the holdfast, the lower unpigmented sections of the thallus often remain comparatively healthy. If damage occurs closer to the base, only stumps of the holdfast remain. Affected lichens are located in two discrete patches characterized by very sharp boundaries with surrounding healthy material of the same species. This study; (i) provides a description of the damaged site, (ii) documents morphological and ultrastructural features of the damage and (iii) compares the photosynthetic pigment composition and chlorophyll fluorescence characteristics of damaged and healthy specimens. Despite massive pruning of the foliose *Usnea* thallus and substantial bleaching of the remaining basal portions (around 80% chlorophyll and carotenoid loss), the results indicate that many of the damaged lichens contain viable algal cells. New shoots are plentiful among many of the remaining lichen stumps. We therefore suggest that the damaged areas described in this paper have the potential for substantial recovery.

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INTRODUCTION

Casey (lat. 66°17′S, long. 110°32′E) is a permanently occupied Australian research station located in the Windmill Islands region of Wilkes Land, East Antarctica (Fig. 1). The northern half of the Windmill Islands region is characterized by low lying rocky outcrops of the Windmill Metamorphics group, a layered sequence of schists, gneisses and migmatites (Blight and Oliver, 1982), separated by areas of permanent snow and ice. The southern half of the region is dominated by the Ardery Charnockite intrusion, with a small area of porphyritic granite (Blight and Oliver, 1982). Glacial erratic boulders and stones, of predominantly metamorphic origin, are widely distributed.

The region supports an abundant and extensive cryptogamic floral community consisting of at least five moss, one hepatic and more than twenty eight lichen taxa (Lewis-Smith, 1986a, 1988; Seppelt, unpublished data). At least ninety soil, snow and freshwater algal taxa are currently being investigated (Ling, 1990, pers. comm). Exposed rock, loose stones and gravel around the new station site and elsewhere within

the region support extensive stands of lichen, of which *Usnea sphacelata* R. Br., *Usnea antarctica* Du Rietz and *Umbilicaria decussata* (Vill.) Zahlbr. are dominant species.

The hill immediately to the south-east of the new station domestic building is well vegetated, but extensive areas of lichen on its north facing slope are seriously damaged. This site was first described by Lewis-Smith (1986b) with the brief statement; 'On this hillside, a dense stand of the lichen *Usnea sphacelata* (= *U. sulphurea*), covering 2 ha, has been almost completely killed by some form of pollution.' He suggested that the most likely cause of damage was contamination by cement dust released during construction of the new station. This area is dominated by *U. sphacelata* with examples of damaged *U. antarctica*, *U. decussata* and *Pseudephebe minuscula* (Nyl. ex. Arnold) Brodo and Hawksworth also present. The most obvious symptom of damage at this site is the loss of the black upper branches of the *U. sphacelata* thalli, leaving only the pale basal sections attached to the rocks and gravel of the substrate.

This study was carried out to obtain baseline data for assessing future vegetation trends, that is, to monitor recovery or further deterioration of the damaged areas. It has four specific aims: to describe the location and extent of the lichen damage described above; to record the symptoms of damage exhibited by the dominant species *U. sphacelata*; to assess the capacity of physically damaged plants for photosynthesis and to compare the findings with those obtained in a similar investigation of airborne alkaline pollution damage to lichens growing downwind of the concrete batching site at Casey (Adamson and Seppelt, 1990).

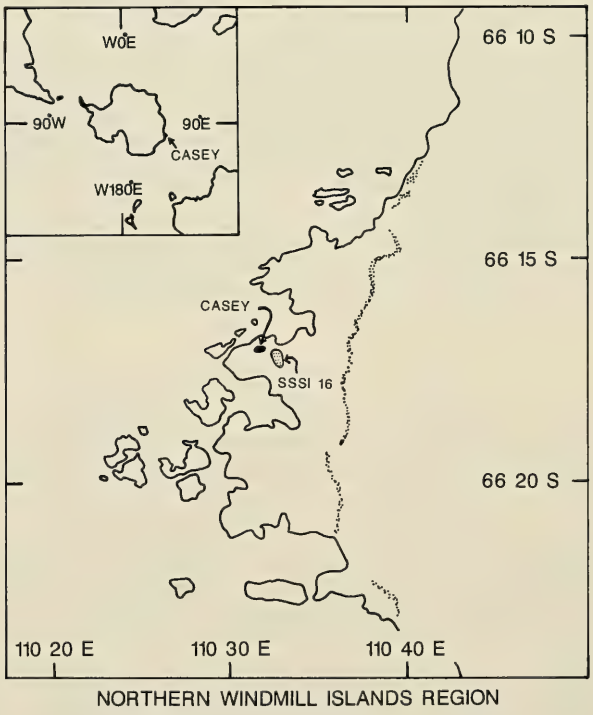

Fig. 1. Location map of Casey Station and the Site of Special Scientific Interest number 16 (S.S.S.I. 16) within the northern Windmill Islands region.

Methods

Preliminary investigations of the morphological features, chlorophyll and carotenoid content and photosynthetic capacity of healthy and damaged *U. sphacelata* were carried out in the field and laboratory at Casey during the summers of 1988-89 and 1989-90. Specimens were also returned to Australia for detailed analysis. They were frozen immediately after collection and kept at -20°C until use. The healthy specimens used for comparative purposes were located in an unaffected control area, 0.5 km to the east of the damaged site, in the Site of Special Scientific Interest number 16 (S.S.S.I. 16).

Pigment Analyses

Photosynthetic pigments (chlorophyll a, chlorophyll b and carotenoids) were extracted into 80% acetone and their concentrations determined using standard spectrophotometric procedures. The control samples were trimmed such that only the lower stem, within 1-2 cm of the holdfast, was compared with samples from the damaged site. Pigment extractions were performed by grinding samples with acid washed sand, 50 mg magnesium carbonate and 10 ml acetone (80%) on ice in dim light. The slurry was transferred to a 10 ml centrifuge tube, shaken vigorously and spun at 2000 rpm for five minutes. The supernatant was then decanted, kept cold and dark, and the pellet resuspended in 1.5 ml acetone (80%) and centrifuged as before. The supernatants were then combined, made up to a known volume and analysed using a scanning spectrophotometer (Hitachi U3200) zeroed at 750 nm. The chlorophyll content was calculated from absorbance values at 663 and 645 nm, according to the equations of Anderson and Boardman (1964) as modified by Brouers and Michel-Wolwertz (1983). The total carotenoid content (per gram dry weight) was calculated from absorbance values at 480 and 510 nm according to Parsons *et al.* (1984). Results are expressed per gram dry weight, calculated from carefully matched samples dried at 80°C for 24 hours.

Fluorescence Measurement

The photosynthetic competence of the algal symbiont, *Trebouxia* sp., in selected representative lichens from both the damaged and control sites was determined using a non-destructive, rapid, chlorophyll fluorescence technique. Comparative field measurements of fluorescence characteristics of damaged and healthy thalli were made using a Branker Plant Productivity Meter (summer 1988-89) and a Biomonitor Plant Stress Meter, S.C.I., AB, Sweden (summer 1989-90). This was followed with further Plant Stress Meter measurements in Australia on frozen material which had been allowed to thaw at 5°C in dim light under moist conditions, for five days. For a technical description of this instrument see Oquist and Wass (1988). The actinic excitation light intensity was set at 300 μmol. m^{-2} sec^{-1} for a period of 10 seconds. A dark adaption time of fifteen minutes was allowed before measurements of initial (Fo) maximum (Fm) and variable (Fv) fluorescence were performed in darkness at 5°C. The principles and techniques of chlorophyll estimation by absorbance spectroscopy and chlorophyll fluorescence analysis are described by Hipkins and Baker (1986) and Lawlor (1987).

Scanning Electron Microscopy

Desiccated specimens were mounted on aluminimum stubs and secured using double sided sticky tape and carbon paint. They were coated with gold using a Polaren E5000 sputter coating unit and viewed in a JEOL JSM 840 scanning electron microscope (SEM). Alternatively, samples were mounted on aluminium tape, sputter coated with carbon and examined in a Philips 505 SEM.

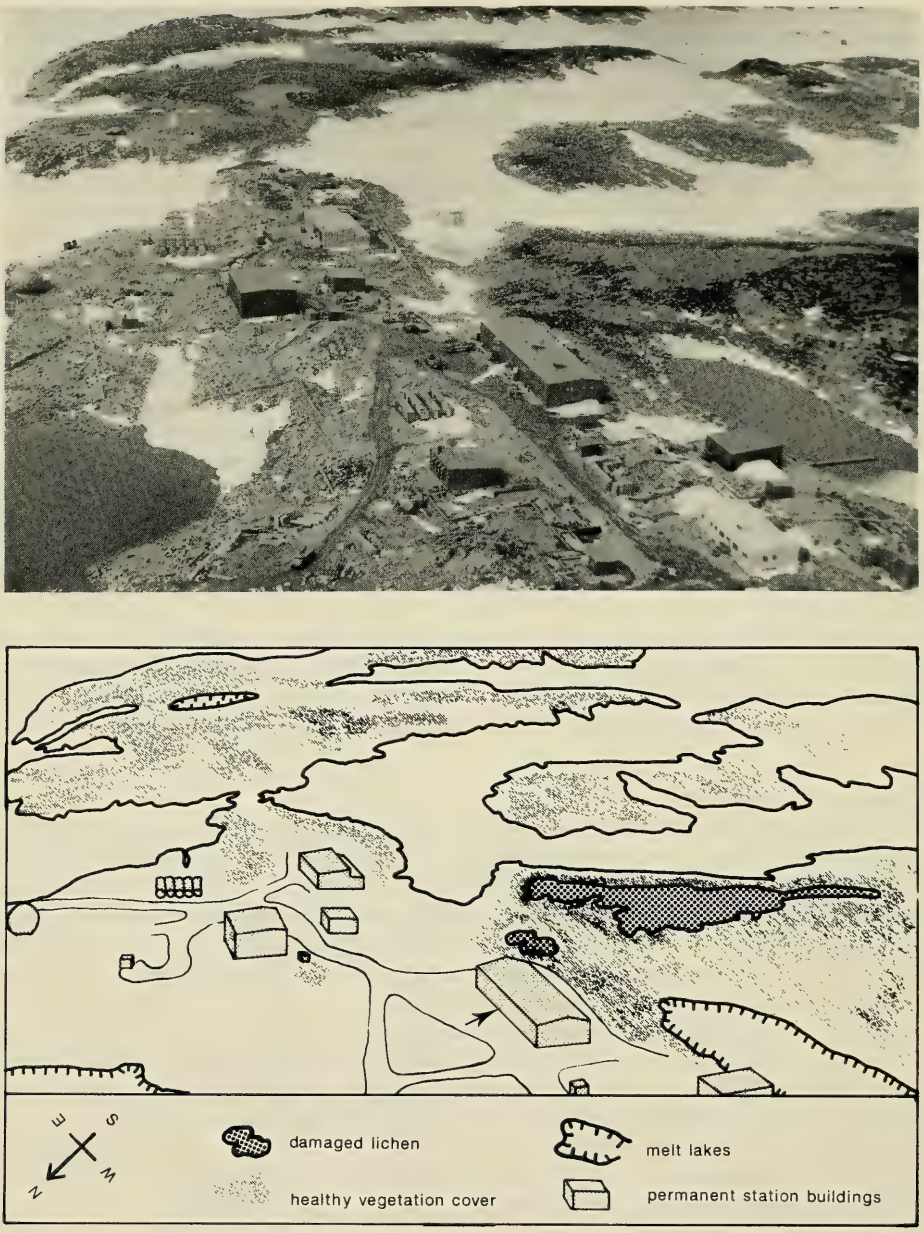

Fig. 2. Casey Station and adjacent areas. (**A**) Oblique aerial photograph showing the two areas of damaged lichen in relation to surrounding healthy vegetation and the eastern half of Casey station. S.S.S.I. 16 includes the well vegetated rocky hills at the top of the photograph. (**B**) Interpretation of the oblique aerial photograph highlighting the two areas of damaged lichen and the extent of surrounding healthy vegetation. Due to foreshortening caused by the oblique nature of the photograph, a scale is not given, but the long axis of the larger patch of damaged lichen is 139 m in length, and the long axis of the smaller damaged patch is 30.5 m in length. Arrow indicates new domestic building.

Transmission Electron Microscopy

Selected thalli were taken from -20°C, placed on moist filter paper in a petri dish and allowed to rehydrate for one hour at 4°C. The thalli were cut into 2-3 mm lengths and fixed in 3% glutaraldehyde in 0.1 M phosphate buffer pH 7.2 at 4°C for 18 hours, washed thoroughly in the buffer and postfixed in buffered 1% OsO_4 for 2 hours at room temperature. The samples were dehydrated in a graded acetone series and embedded in a low viscosity epoxy resin. Thin sections were stained sequentially in uranyl acetate and lead citrate and examined in a Philips 400 transmission electron microscope (TEM).

Soil pH

Soil pH was determined at the larger affected site for comparison with soil samples from S.S.S.I. 16 and other unaffected sites further from the station. Soil was collected to a maximum depth of 3 cm, dried and sieved through a 2 mm pore size soil sieve. 10 g of dry soil was then mixed with 50 ml ultrapure water (Milli-Q filter, Millipore) agitated on an orbital shaker for 10-15 minutes and pH measurement of the soil water slurry made with plastic pH strips (Merck Universal Indikator). A comparison using a portable pH meter (TPS LC 80) indicated that this method underestimates soil pH values by 0.28 +/- 0.08 pH units.

Results

Descripton of the Affected Site

There are two distinct areas of apparenty bleached *Usnea* lichen which have lost the upper sections of their thalli (Figs 2**A**, **B**). Both are characterized by sharp but irregular boundaries with surrounding healthy lichen. The larger of the two areas covers approximately 6600 m^2 on the north facing side of the hill located immediately to the south-east of the new domestic building. This area is composed of an extensive slope of predominantly small stones, with scattered larger boulders. The damaged lichen occurs on both small and large rocks. The smaller affected area is approximately 360 m^2, dominated by large boulders and located on relatively level ground at the base of the affected slope. The two patches are separated by approximately 25 metres of similar rocky terrain vegetated with undamaged lichen and moss. Within each affected area, there are scattered small patches that appear unscathed. These often, but not exclusively, occur in sheltered areas in the lee of rocks and hollows. There may be some correlation between the location of these apparently healthy patches and snowdrift patterns or protection from the strong, predominantly easterly winds. The removal of the black upper sections of the damaged *U. sphacelata* makes the affected areas quite obvious. In the oblique aerial photograph (Fig. 2**A**) they can be clearly distinguished as pale patches surrounded by black areas of healthy lichen. These sites are not subject to vehicular or extensive foot traffic and do not appear to have been physically disturbed. Soil pH at the larger of the two affected sites was found to be 4.4, consistent with the regional mean of pH 4.

Symptoms of Damage to U. sphacelata

A comparison of typical healthy and damaged specimens of *U. sphacelata* is shown in Fig. 3. In the damaged specimens, the heavily pigmented upper parts of the thalli are missing, the remaining lower sections are somewhat bleached near the shear zone and the central strand frequently protrudes beyond the remaining medulla and cortex. The length of the remaining lower sections varies, but in most cases, the upper branches appear to have been sheared off at a uniform level (Figs 3, 4**A**, **B**). Where the holdfast

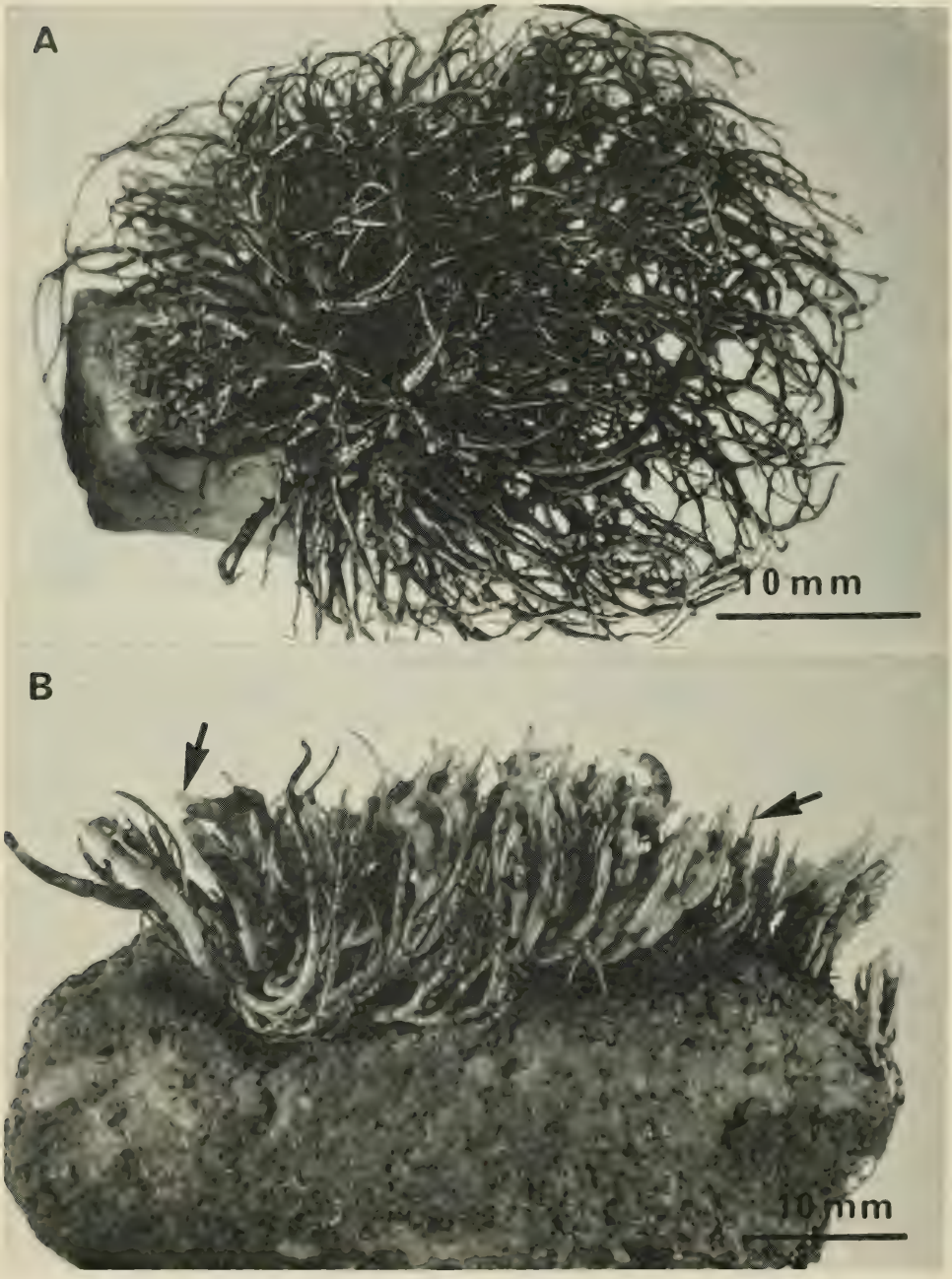

Fig. 3. Typical examples of (**A**) healthy and (**B**) damaged *U. sphacelata* from the S.S.S.I. 16 control site and the larger of the two damaged areas to the south-east of the new station domestic building. Note the heavily pigmented branching thallus of the healthy sample compared to the 'shaved' remnant thallus of the damaged sample with its upper branches missing and the central strand frequently protruding.

and lower sections of the lichen are growing from the underside of small rocks on the extensive gravel slope, the shear zone frequently corresponds with the level at which the lichen appears above the protection of surrounding rocks. The lower sections often appear to remain comparatively healthy although the cortex may split (Fig. 4**C**). In many samples, the shear zone occurs well above small intact branches in the region of the holdfast. These do not seem to be damaged and some may represent growth subsequent to the damage that has affected the rest of the lichen. It is also possible for one section of a lichen to be severely damaged while a significant portion appears totally unaffected. In the majority of cases, the holdfast and lower branches remain firmly attached. Similar symptoms of mild damage have occasionally been observed in isolated samples of *U. sphacelata* in areas remote from this site, but the severity and extent of damage at this site is unique.

Initial observations made with a dissecting microscope were sufficient to confirm the presence of cells of the algal symbiont *Trebouxia* sp. within many of the remaining damaged lichen stems. They were also particularly obvious in small undamaged shoots growing near the holdfast. The transmission electron micrographs in Fig. 5 are consistent with an apparently healthy algal fungal symbiotic relationship and healthy algal cells close to the base of severely damaged specimens. After several days in warm, moist laboratory conditions, there was a marked increase in the algal content of the damaged lichens indicating rapid reproduction of algal cells in favourable conditions.

Results of the photosynthetic pigment analyses carried out on samples taken from the basal 1-2 cm of thalli from control and damaged sites are listed in Table 1. Healthy specimens from the control site contained approximately six times as much chlorophyll and carotenoid pigments as damaged specimens. The ratio of carotenoids to chlorophyll did not vary significantly between the sites. However, the mean chlorophyll a/b ratio was significantly lower for the damaged specimens (3.7 verses 4.6). In all cases, the standard error values are low indicating consistency within each site.

TABLE 1

Chlorophyll and carotenoid content of basal sections of damaged and control samples of U. sphacelata. *Freshly collected samples were extracted and measured in Antarctica*

Pigment Content/Ratio	Damaged *U. sphacelata* (n = 10)	Control *U. sphacelata* (n = 10)
total chlorophyll (ug chl/g dry wt):	43.22 +/- 5.89	266.66 +/- 12.33
chlorophyll a/b ratio:	3.67 +/- 0.21	4.62 +/- 0.10
total carotenoids (ug carot/g dry wt.):	23.75 +/- 2.99	143.95 +/- 7.30
carotenoid/chlorophyll ratio:	0.55 +/- 0.01	0.54 +/- 0.004

Photosynthetic Status of Damaged U. sphacelata

Samples from the damaged lichen site demonstrated an active photosynthetic response to the Plant Stress Meter II probe. The mean initial (Fo), maximum (Fm) and variable fluorescence (Fv) values, and the mean ratio of variable fluorescence to maximum fluorescence (Fv/Fm) of the damaged and control samples are listed with standard errors in Table 2. In comparison with the control samples, the damaged lichen exhibits reduced values of Fo, Fm and Fv, but the Fv/Fm rato is not significantly different (Fv/Fm: 0.422 +/- 0.021 and 0.435 +/- 0.015 respectively).

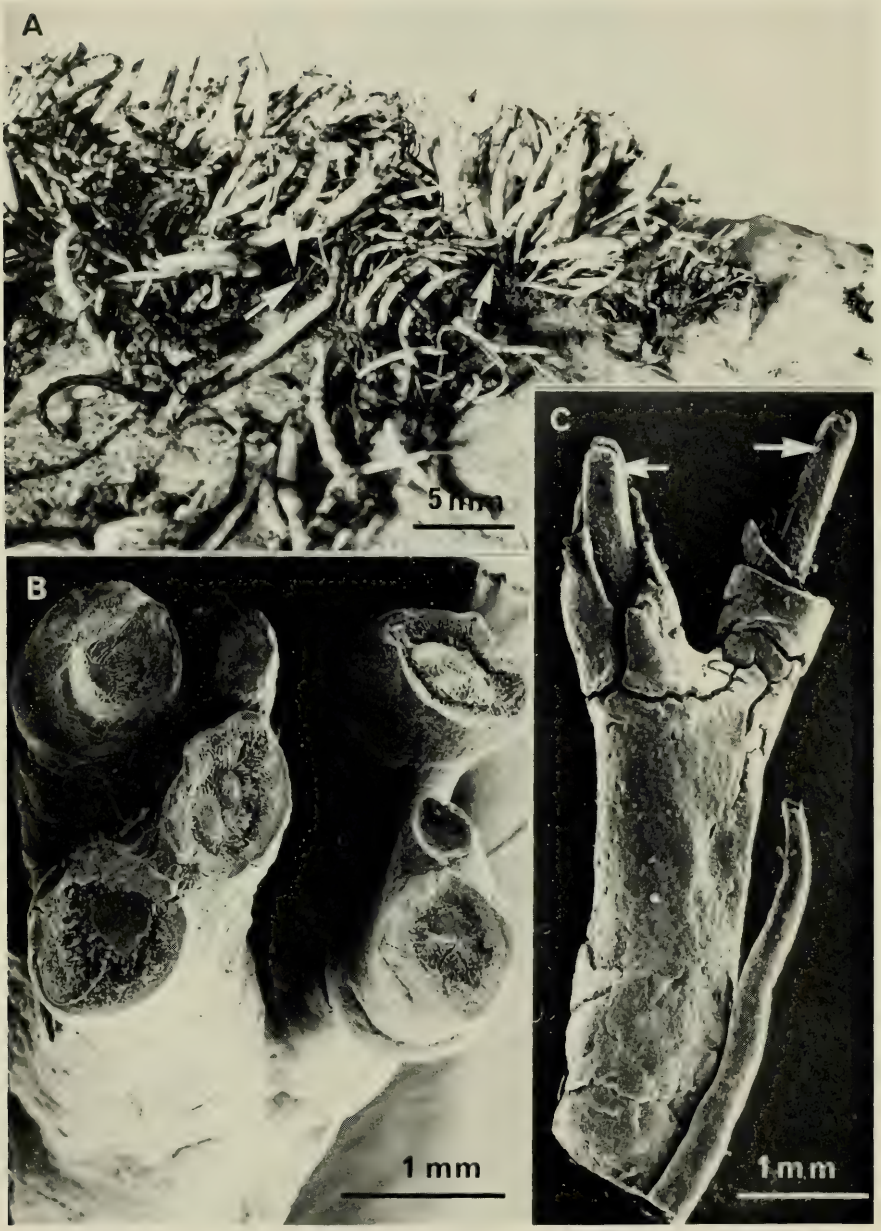

Fig. 4. Damaged *U. sphacelata*; (**A**) remaining basal sections of damaged lichen with numerous small intact shoots, (**B**) SEM showing the clear breaks of naturally 'shaved' thalli, (**C**) SEM of basal section of damaged thallus with central strand protruding.

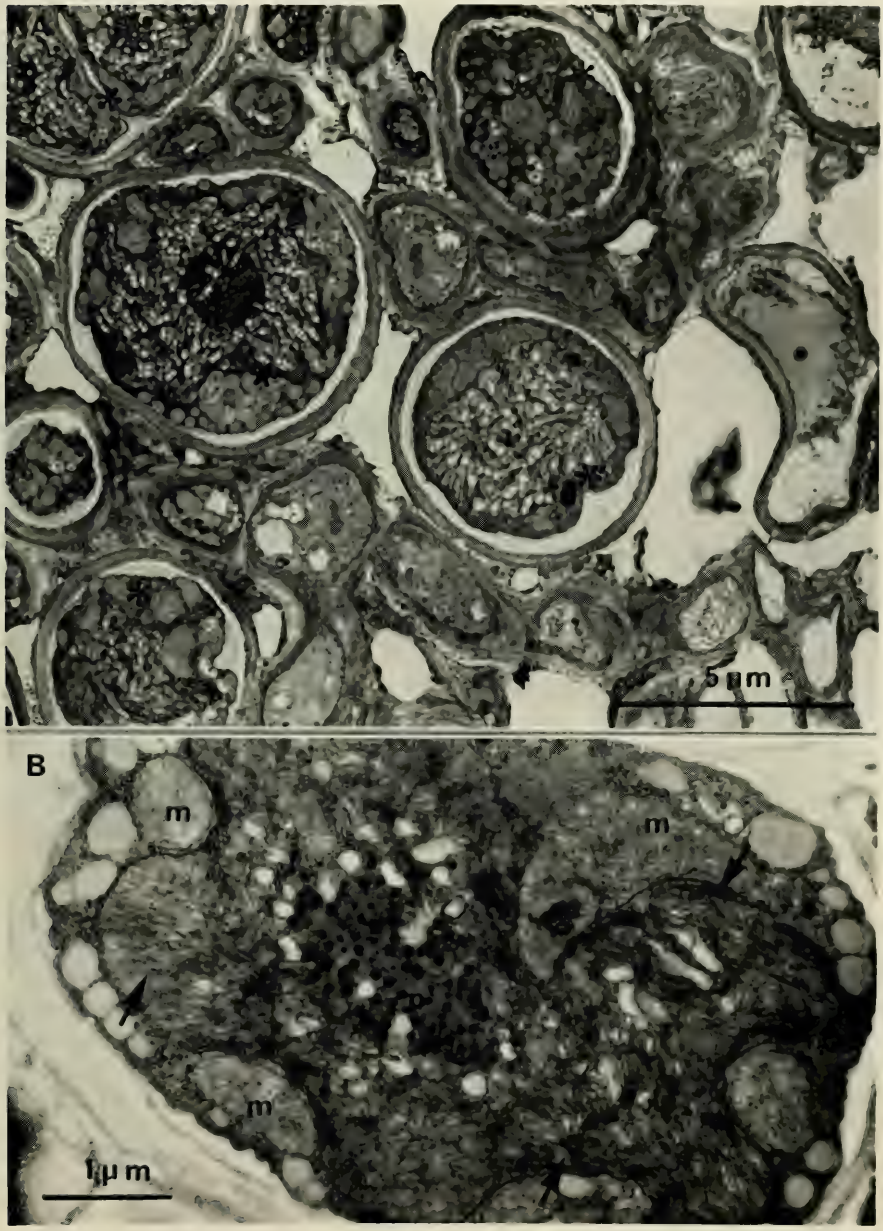

Fig. 5. TEM of damaged *U. sphacelata* showing: (**A**) transverse section of thallus close to the holdfast (phycobiont = asterisk), (**B**) transverse section of algal cell; chloroplast central pyrenoid = p, thylakoids = arrow, and mitochondria = m.

TABLE 2

Chlorophyll fluorescence at 5° C of damaged and control samples of U. sphacelata. *The experiment was performed in Australia on material which had been kept frozen at -20° C*

Fluorescence Values	Damaged *U. sphacelata* (n = 20)	Control *U. sphacelata* (n = 23)
Initial fluorescence (Fo):	0.163 +/- 0.013	0.280 +/- 0.030
Maximum fluorescence (Fm):	0.297 +/- 0.029	0.536 +/- 0.072
Variable fluorescence (Fv):	0.135 +/- 0.018	0.256 +/- 0.043
Variable fluorescence / Maximum fluorescence (Fv/Fm):	0.422 +/- 0.021	0.435 +/- 0.015

DISCUSSION

Chlorophyll fluorescence is a sensitive indicator of the photosynthetic competence of plants and has been widely used to monitor photosynthetic activity in field situations and to register plant responses to stress (Hetherington *et al.*, 1989; Hetherington and Oquist, 1988; Ögren, 1988). Variable fluorescence (Fv) originates from the pigments of photosystem II and is related to the availability of electron accepting quinone molecules. When these are all reduced, fluorescence is maximal (Fm). The ratio of Fv/Fm is proportional to the photochemical efficiency of photosystem II and correlates very well with the quantum yield of net photosynthesis (Oquist and Wass, 1988). An Fv/Fm ratio of around 0.8 is typical for C_3 higher plants under ideal conditions (Bjorkman and Demmig, 1987). Mean Fv/Fm ratios of around 0.4 for *U. sphacelata* from both the control and damaged sites indicates that the photosynthetic efficiency of the algal symbionts in the healthy and in many of the damaged lichens are similar, and that both experienced a similar degree of stress (possibly due to less than optimal hydration conditions) during the experiment reported in Table 2. It is not yet clear why the fluorescence yield with all reaction centres open (Fo) and the variable (Fv) and maximum (Fm) fluorescence values are significantly lower in the damaged thalli. Differences in the physical properties of the mycobiont surrounding the algal cells and the concentration of photoprotective lichen pigments may be relevant.

The presence of healthy cells of the algal symbiont *Trebouxia* sp. in the lower fronds of many of the damaged lichens was confirmed by electron microscopy. The algal cells in the basal 10 mm or so of the damaged remnant thalli were indistinguishable from those of healthy lichens. The essentially identical carotenoid to chlorophyll ratios in lichens from affected and control sites is also consistent with the presence of healthy algal cells in physically damaged specimens. Although the damaged lichens contain normal, photosynthetically competent *Trebouxia*, their mean chlorophyll and carotenoid concentrations are very low compared to those of the lower 1-2 cm sections of control lichens. This is mainly due to a lower concentration of algal cells. We do not however, discount the possibility that the total chlorophyll and carotenoid concentrations per cell are also reduced. A possible explanation for the lower chlorophyll a/b ratio in damaged plants is that it is a response to increased light intensity following loss of the upper heavily pigmented branches of the thallus which normally shade the paler lower regions.

The severity and extent of the damage to lichens described in this study is unique in the Windmill Islands region. Smaller isolated examples of sheared *U. sphacelata* have been observed in areas remote from the station, but the damage has not been severe or widespread, affecting only occasional isolated lichens. In the more distant examples, the shear zone is located well above the holdfast in the black pigmented areas of the upper

fronds and the damaged lichens are not so easily distinguished from surrounding healthy material by colour.

Despite the close proximity of these large affected areas to the new station, there is as yet no direct evidence to link the damage directly to events that have occurred due to construction activities or other human impact. The cause of damage is unknown. Since the soil pH in the affected area is low (pH 4) and consistent with the surrounding mean, it is most unlikely that the damage was caused by pollution by alkaline cement dust. In contaminated areas downwind of the concrete batching site the soil is alkaline, with values up to pH 9 (Adamson and Seppelt, 1990). A separate study of alkaline pollution in this area has shown that *U. sphacelata* affected by cement dust pollution is typically bleached, shrivelled and in many cases weakened or detached at the holdfast (Adamson and Seppelt, 1990). These symptoms of damage are quite different to those found in the areas described in this paper.

Disease, toxic fumes and physical abrasion have also been suggested as possible causes of damage. Disease seems unlikely as there is no evidence of viral or bacteriological infection or invasive fungi in the electron-micrographs. A catastrophic leak of poisonous fumes and an inconsistent snow cover could explain the distribution of small scattered healthy patches within the affected areas. Physical abrasion by ice, soil and rock particles carried by a particularly strong wind event may be a natural explanation for the damage consistent with occasional isolated examples of similar damage in other locations and with patchy snow or ice cover protecting some areas within the damaged sites. It is however difficult to explain the sharp boundaries with surrounding healthy material and the existence of two discrete affected areas. There may of course have been a combination of factors resulting in this damage, for example chemical contamination or disease could make the lichens more susceptible to physical abrasion by airborne particles.

The presence of numerous young and still mainly unbranched thalli amongst the damaged remains of a previously flourishing stand of mature *U. sphacelata* indicates that the damaged areas to the south-east of the new station domestic building are now recovering. It also implies that the damage was caused by a catastrophic event and is not symptomatic of an ongoing chronic pollution problem at Casey Station.

Acknowledgements

This project was funded by grants from th Antarctic Science Advisory Committee and the Macquarie University Research Grants Scheme. We thank the Australian Antarctic Division for logistic support and supply of technical equipment in Antarctica, Mr. Peter Orbansen and Mr. Seton (Australian Construction Services) for Fig. 2**A** and assistance in the field, Mr. Ron Oldfield (Macquarie University) for Fig. 3, Mr. Tom Joyce (Electron Microscope Unit, University of Sydney) for Fig. 4**A**, Ms. Sue Doyle (Macquarie University) for Fig. 4**B** and Mr. Peter Vesk (Electron Microscope Unit, University of Sydney) for Fig. 4**C**.

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THE LINNEAN SOCIETY OF NEW SOUTH WALES

Record of the Annual General Meeting, 1988

The one hundred and thirteenth Annual General Meeting was held in the Seminar Room, Royal Botanic Gardens, Sydney, on Wednesday, 30th March 1988, at 6.00 p.m.

The President, Dr P. M. Martin, occupied the Chair. The minutes of the one hundred and twelfth Annual General Meeting were adopted by the members present.

Report on the Affairs of the Society for the Year 1987-88

Publications

The Society's *Proceedings* were published as follows:—

Volume 109, Nos 3 & 4 December 1987

Professor T. G. Vallance continues to donate his time and expertise to editing the *Proceedings*, with great financial benefit to the Society.

Back issues (Volumes 1-100) of the *Proceedings* have been sold at bargain prices during the year. This special offer will terminate at the end of 1988, when remaining surplus stock will be destroyed, thus relieving the Society of the expense of storage.

We are indebted to Mr Alan Andrews, a Council member, who has generously given his time and effort to pack and despatch the orders for back issues. The President, Dr Peter Martin, has also donated his time and energy to the gathering and packing of orders for sets of *Proceedings*, as complete as possible, for institutional libraries. We also thank members who have sent us back issues which they no longer require. Some of these have helped to make sets more complete.

Newsletter

Dr Helene Martin continues to edit the Linnean Society Newsletter, which was published quarterly throughout the year and distributed to all members. It included details of our Programme, summaries of some lectures, reports of Council resolutions, titles and authors of papers accepted for publication in the *Proceedings*, details of research grants and other items of interest to members.

Membership

On March 29th we had 236 Full Members and 25 Associate Members, making a total of 261 members.

The decrease in the number of members registered this year is due to the necessity for a firmer approach to the removal of names of unfinancial members.

We offered congratulations to Professor Michael Archer in May when he was awarded the first Queensland Museum Medal for contributions to research in Queensland in fields relevant to the Queensland Museum.

We record with regret the deaths of two distinguished past presidents during the year. Ivor Vickery Newman, M.Sc. (Sydney), Ph.D. (London), F.L.S., F.R.M.S., president 1960-61 and a member since 1925, died in Sydney on 5th May 1987. On 5th October 1987, Lilian Ross Fraser, D.Sc. (Sydney), president 1948-49 and 1957-58 and a member since 1930, died at Hornsby hospital after a long illness.

Meetings

All meetings this year, except the Macleay Memorial Lecture, were held at the Royal Botanic Gardens, Sydney, by kind permission of the Director, Professor T. C. Chambers.

A joint meeting with the Antarctic Society of Australia was held on 4th June 1987, when Dr Patricia Selkirk of Macquarie University and Dr D. S. (Woody) Horning of the Macleay Museum reported on a recent symposium on 'Macquarie Island — Past, Present and Future', organized by the Antarctic Division, Australian Department of Science.

On 1st July, Dr Pat Quilty of the Antarctic Division, Department of Science, spoke on the topic 'Pliocene Antarctic Vertebrate and Wood Remains and their significance for the Development of Antarctic Glaciation'.

The Fifteenth Sir William Macleay Memorial Lecture was delivered on 30th September at the Australian Museum, Sydney. A lecture entitled 'The Elastic-sided Gumleaf, or: The Rubber Cuticle and other Studies of the *Corymbosae*' was prepared by D. J. Carr and S. G. M. Carr and delivered by Emeritus Professor D. J. Carr. [The text of this lecture has been published in the *Proceedings* (110(2), (1987) 1988: 101-140).]

On 21st October, Professor W. Schofield, Department of Botany, University of British Columbia, spoke on the topic 'The Biogeography of Bryophytes'.

On 11th November, Dr K. Y. Cho, Linnean Macleay Lecturer in Microbiology at the University of Sydney, gave a talk on 'The Biotechnology of Mushroom Cultivation'. This was followed by a mushroom tasting and a mushroom dinner of several courses, prepared by Dr Helene Martin.

On 28th January 1988, Dr Robert Hill from the School of Botany, University of Tasmania, spoke on the topic 'Evolution of the Tasmanian Vegetation — Forty Million Years of Evidence'.

Our customary informal luncheon for members and friends preceded the first Council meeting of the year, on 17th February.

The Joyce W. Vickery Scientific Research Fund

Fifteen grants totalling $7,160 were awarded this year. Details are recorded in Newsletter No. 46 (October, 1987).

Linnean Macleay Fellowship

It was decided at the Council Meeting held on 17th February, 1988 that, as Ms Julia Hush had satisfied the requirements of her appointment in 1987, her Fellowship would be renewed for 1988.

Office

The Society's office continues to operate from 6/24 Cliff Street, Milsons Point, and is open from 9.30 a.m. to 5 p.m. every Tuesday. The telephone number is (02) 929 0253.

Linnean Macleay Lectureship in Microbiology

Dr Cho continued working on (1) the development of slow release supplement used for increasing mushroom yield and (2) the effect of light and carbon dioxide in the morphogenesis of *Flammulina velutipes*. The two well-equipped mushroom houses financed by the N.S.W. Department of Industrial Development and Decentralization were completed and have since been in continued use. He is a member of the seven-member Organization Committee for the International Symposium on Mushroom Biotechnology to be held in China November, 1989.

Presidential Address

The President, Dr P. M. Martin, delivered an address entitled 'The Future of the Introduced Element of the Australian Flora'.

Synopsis

The focus of the address was the status of the introduced element of the Australian Flora, with particular reference to the grass genus *Phalaris* and the leguminous genera *Trifolium* and *Medicago*.

Migration, through both natural and human agencies, has played an important part in the addition of species to the Australian flora, but prior to 1788 the significance of the human agencies was probably very limited.

New arrivals may or may not succeed in establishing themselves in the wild, but if they do manage to persist for a reasonable number of years they are then described as 'naturalized species'. The main question posed in this address is whether some naturalized species have reached the point at which they could be regarded as having been assimilated into the Australian flora on a permanent basis.

Evidence was presented to show that a wide variety of levels of integration exist. Some introductions, especially in those parts of the continent characterized by open woodland formations, have reached a level of integration which renders a continuation of human activities unnecessary for their long term survival. Indeed, in some communities the naturalized species seem to be the controlling elements. At the other extreme are species which would quickly disappear if quite small changes were to be made in farming practices.

Attention was drawn to the frequent lack of detailed information on the dynamics of vegetational change in Australia, a situation which makes comments about future directions for the majority of the more recently introduced species difficult to formulate with any degree of certainty. This neglect is related in considerable measure to a tendency to regard species which have become naturalized since 1788 as intruders, regardless of the status of these species in the present-day vegetation.

Declaration of Elections

As the number of nominations did not exceed the number of vacancies, no ballot was necessary. The President declared the following members elected:

President	—	Professor T. G. Vallance
Members of Council	—	Dr M. R. Gray
		Dr S. J. Hand
		Dr D. S. Horning
		Dr H. A. Martin
		Dr J. Pickard
		Dr A. Ritchie
Auditor	—	W. Sinclair & Co.

Note on Accounts for 1987

Due to circumstances beyond the control of the Honorary Treasurer, audited accounts for the year were not available for presentation at the Annual General Meeting 1988. The accounts printed in this Annexure were eventually approved by Council after the auditor had completed his work.

LINNEAN SOCIETY OF NEW SOUTH WALES

GENERAL ACCOUNT

Balance Sheet as at 31st December, 1987

1986			1986			
$		$	$		$	$
	Accumulated Funds—			Fixed Assets—		
	Balance 1st January, 1987	160,512.88		Furniture, Fixtures & Fittings — At Cost	1,947.91	
	Add Surplus for Year	22,867.30	957	*Less* Depreciation written off	1,055.37	892.54
	Sale of Gould book monographs	71,500.00				
	Increase in Value of Assets	549.50		Office Machines — At Cost	4,943.88	
			2,927	*Less* Depreciation written off	2,455.88	2,488.00
160,513	Balance 31st December, 1987	255,429.68				
			3,884	Total Fixed Assets		3,380.54
230	Library Fund	677.00				
	Reserve—					
1,143	Bookbinding	1,142.66		Investments—		
				Deposits—		
$161,886		$257,249.34	23	Advance Bank Australia Ltd	24.87	
			—	Australian Guarantee Corp. Ltd	5,000.00	
			39,500	Australian Resources Development Ltd	—	
			20,526	Australian Savings Bonds — At Cost	20,526.00	
			8,000	N.S.W. Premier State Bonds — At Cost	8,000.00	
			5,000	Westpac Banking Corporation	118,057.61	
				Debentures — At Cost		
			9,300	Custom Credit Corporation Ltd	59,300.00	
			13,700	Esanda Ltd	13,700.00	
			96,049	Total Investments		224,608.48
				Current Assets—		
			4,323	Sundry Debtors	1,518.92	
			2,162	Linnean Macleay Fellowships Account	—	
			55,318	Cash at Bank	27,591.40	
			150	Deposit	150.00	
			61,953	Total Current Assets		29,260.32
			$161,886	Total Assets		$257,249.34

LINNEAN SOCIETY OF NEW SOUTH WALES

Income & Expenditure Account for the Twelve Months ended 31st December, 1987

1986			1986			
$		$	$		$	$
	EXPENDITURE			INCOME		
900	Audit Fees	950.00		Subscriptions—		
78	Bank Charges	138.51	1,845	Members	2,387.50	
480	Depreciation	503.00	8,840	Proceedings	6,124.53	
501	General Expenses	856.43	10,685			8,512.03
309	Insurance	170.15	15,256	Interest Received		23,339.73
202	Light and Power	211.92		Fellowship Account—		
94	Newsletter Expense	227.26		Surplus Income for the year ended		
1,163	Postages	1,649.67	12,576	31st December, 1987		10,271.49
7,296	Proceedings — Printing Costs	7,671.55	220	Donations Received		—
433	Printing and Stationery	1,272.02		Reprints Sales		
5,253	Rent	4,995.00	885	General	819.12	
—	Photocopying Expenses	60.00	2,798	Polychaete Vol.	480.54	1,299.66
5,460	Salaries	6,279.00				
2,334	Secretarial Services	2,927.38	—	Sales — Back Issues		7,675.27
225	Telephone	318.99	$42,420	Total Income		$51,098.18
$24,728	Total Expenditure	$28,230.88				
	Surplus for Year Transferred to					
$17,692	Accumulated Funds	$22,867.30				

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the twelve months ended 31st December, 1987 and are of the opinion that the accompanying Balance Sheet and Income and Expenditure Account correctly sets forth the position of the financial affairs as at 31st December, 1987 according to the explanations given to us and as disclosed by the Books of the Society.

W. SINCLAIR & CO.
Chartered Accountants
Registered under the Public Accountants Act, 1945, as amended.

DATED at Sydney this Twenty Seventh Day of April, 1989.

I. G. PERCIVAL
Hon. Treasurer.
27th April, 1989.

LINNEAN SOCIETY OF NEW SOUTH WALES

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT

Balance Sheet as at 31st December, 1987

1986 $			$	1986 $		$
	Accumulated Funds—				Investments—	
	Balance 1st January, 1987			5,132	Australian Savings Bonds — At Cost	5,131.50
	Amount bequeathed by Sir William Macleay	70,000.00		55,300	N.S.W. Premier State Bonds At Cost	55,300.00
	Transfers from Income Account	59,873.10			Debentures — At Cost	
	Increase in Value of Assets	384.32	130,257.42	5,000	Beneficial Finance Corp. Ltd	5,000.00
	Less Adjustment of Transfers to General Account in respect of Interest Received		318.69	200	British Petroleum Company of Aust. Ltd	200.00
			129,938.73	700	Custom Credit Corporation Ltd	700.00
	Less Decrease in Assets		881.37	18,800	Esanda Limited	18,800.00
					Deposits—	
129,939	Balance 31st December, 1987		129,057.36	—	Australian Guarantee Corp. Ltd	35,400.00
	General Account—			16,200	Australian Resources Development Bank	—
2,162	Interest not Transferred		—	2,673	St George Building Society Ltd	2,859.22
				625	Advance Bank Australia Ltd	666.64
$132,101			$129,057.36	27,400	Westpac Banking Corporation	5,000.00
				132,030	Total Investments	129,057.36
					Current Assets—	
				39	Cash at Bank	—
				32	Sundry Debtors	—
				71	Total Current Assets	—
				$132,101		$129,057.36

Income and Expenditure Account for the Twelve Months ended 31st December, 1987

3,200	Salaries	3,200.04	15,776	Interest Received	13,471.53
$12,576	Surplus for the Year transferred to General Account	$10,271.49			

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the twelve months ended 31st December, 1987 and are of the opinion that the accompanying Balance Sheet and Income and Expenditure Account correctly sets forth the position of the financial affairs of the Linnean Macleay Fellowships Account as at 31st December, 1987 according to the explanations given to us and as disclosed by the Books of the Society.

W. SINCLAIR & CO.
Chartered Accountants
Registered under the Public Accountants Registration Act, 1945, as amended.

DATED at Sydney this Twenty Seventh Day of April, 1989.

I. G. PERCIVAL.
Hon. Treasurer.
27th April, 1989.

LINNEAN SOCIETY OF NEW SOUTH WALES

BACTERIOLOGY ACCOUNT

Balance Sheet as at 31st December, 1987

1986 $		$	$	1986 $		$
	Accumulated Funds—				Investments—	
	Balance 1st January, 1987			26,900	N.S.W. Premier State Bonds — At Cost	26,900.00
	Amount Bequeathed by Sir William Macleay	24,000.00			Debentures—	
36,900	Transfers from Income Account Etc.	12,900.00	36,900.00	—	Australian Guarantee Corporation	8,590.00
	Macleay Lecturer in Microbiology Reserve—			200	British Petroleum Company of Aust. Ltd	200.00
	Balance 1st January, 1987	1,284.28		1,600	Esanda Ltd	1,600.00
	Add Surplus for Year	4,350.38			Deposits—	
				454	Advance Bank Australia Ltd	484.64
1,284	Balance 31st December, 1987		5,634.66	8,000	Westpac Banking Corporation	—
$38,184			$42,534.66	37,154	Total Investments	37,774.64
					Currents Assets—	
				985	Cash at Bank 4,715.28	
				45	Sundry Debtors 44.74	
				1,030	Total Current Assets	4,760.02
				$38,184		$42,534.66

Income & Expenditure Account for the Twelve Months ended 31st December, 1987

5,000	University of Sydney — Salary of Lecturer	—	4,286	Interest Received 4,350.38
$ (714)	Surplus for Year	$4,350.38		

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the twelve months ended 31st December, 1987 and are of the opinion that the accompanying Balance Sheet and Income and Expenditure Account correctly sets forth the position of the financial affairs of the Bacteriology Account as at 31st December, 1987 according to the explanations given to us and as disclosed by the Books of the Society.

W. SINCLAIR & CO.
Chartered Accountants
Registered under the Public Accountants Registration Act, 1945,
as amended.

DATED at Sydney this Twenty Seventh Day of April, 1989.

I. G. PERCIVAL.
Hon. Treasurer.
27th April, 1989.

LINNEAN SOCIETY OF NEW SOUTH WALES

JOYCE W. VICKERY SCIENTIFIC RESEARCH FUND ACCOUNT

Balance Sheet as at 31st December, 1987

1986				1986		
$		$	$	$		$
	Accumulated Funds—				Investments—	
	Balance 1st January, 1987	91,935.22		5,132	Australian Savings Bonds — At Cost	5,131.50
	Interest Received	8,804.66		20,000	N.S.W. Premier State Bonds — At Cost	20,000.00
		100,739.88			Debentures—	
	Less Research Grants	8,535.24		12,258	Australian Guarantee Corp. Ltd	17,000.00
				1,200	British Petroleum Company of Aust. Ltd	1,200.00
91,935	Balance 31st December, 1987		92,204.64	11,000	Citicorp	—
	Current Liabilities—			18,000	Custom Credit Corporation Ltd	18,000.00
132	Sundry Creditors	—		13,000	Esanda Ltd	13,000.00
1,277	General Account	—	—		Deposits—	
$93,344			$92,204.64	154	St George Building Society	165.23
				12,600	Westpac Banking Corporation	15,100.00
				93,344	Total Investments	89,596.73
					Current Assets—	
				—	Cash at Bank	2,607.41
				$93,344		$92,204.14

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the twelve months ended 31st December, 1987 and are of the opinion that the accompanying Balance Sheet correctly sets forth the position of the financial affairs of the Scientific Research Fund Account as at 31st December, 1987 according to the explanations given to us and as disclosed by the Books of the Society.

W. SINCLAIR & CO.
Chartered Accountants
Registered under the Public Accountants
Registration Act, 1945, as amended

DATED at Sydney this Twenty Seventh Day of April, 1989.

I. G. PERCIVAL.
Hon. Treasurer.
27th April, 1989.

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Issued December, 1990

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